Systematic Zoology

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Squirrel Geography of the Indian Subregion

JOSEPH CURTIS MOORE

Introduction

IT HAS sometimes been said that when a taxonomist completes a revision of a group, much may be lost if the bearing of the presumably firmer knowledge thus attained on the biogeography of the region is not commented upon by the reviser himself. However applicable this may be generally, it appears to the writer that this is true of diurnal squirrels (Sciurinae). Having completed, as a part of a larger study, revision of the Sciurinae of the Indian Subregion, the writer offers here the pertinent evidence and a bit of speculation.

Garo-Rajmahal Gap

The most important zoogeographic barrier in the Oriental Region is the Garo-Rajmahal Gap. This is the 125-mile span of the Ganges and Bramaputra delta that separates the Garo Hills on the east from the Rajmahal Hills on the west. The Rajmahal Hills (under 1500 feet elevation) connect with a chain of hills that extends across central India, continuously

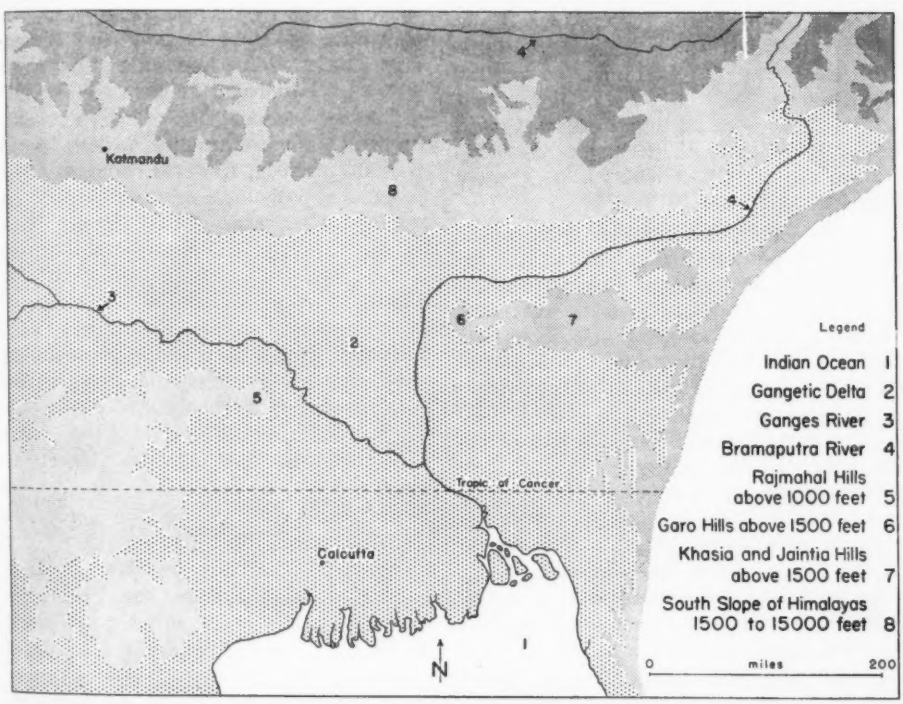

FIG. 1. The Garo-Rajmahal Gap between the Indian faunal subregion and the Indochinese faunal subregion.

maintaining elevation above 1000 feet and often rising above 3000 feet, to the north end of the higher hill ranges collectively known as the Western Ghats that extend along the western edge of peninsular India. Many species of vertebrates occurring in the cool, high rainforests of the Western Ghats have close relatives in the Himalayas or the hill country of Assam 1000 miles to the east, and in between occur only spottily on a few high hills or not at all.

Satpura Hypothesis

Explanation of such disjunct distributions has led to the Satpura hypothesis stoutly advocated by Hora (1949, and see the 13 papers by other authors published, together with this and six other papers by Hora, as a symposium on the Satpura hypothesis). Coördinate with the Garo-Rajmahal Gap as a faunal barrier, is the near desert condition of north-central India, extending from the western Himalayas southward down the middle of the peninsula (see, for example, the rainfall distribution map p. 358, Anonymous, 1949). This near desert prevents spread of forest forms from the rainforest strip on the face of the Himalayas southward into India.

Hora's (1949, p. 313) statement of the Satpura hypothesis indicated that he considered three conditions fundamental to it: 1) former continuity of the east-west chain of hills (including the Satpuras) across central India from the Western Ghats to the Garo Hills. 2) former maximum elevation above sea level of five to six thousand feet of these hills and of the northern part of the Western Ghats (considered necessary to provide a continuous belt of rainforest under climatic conditions such as prevail now). 3) a Pleistocene age of the origin of the Garo-Rajmahal Gap, presumably by block-faulting (only implicit in Hora's 1949 paper, but stated in his 1944 paper, p. 432).

In a quite technical geological paper Auden (1949) considers the Satpura Hypothesis at some length and concludes that: "The evidence is not in favour, therefore, of the conception of a major Ur-Satpura range extending across [central] India during the Tertiary period that has subsequently been worn down to the present elevations." This will not admit Hora's fundamental condition number two above. For explanation of the evidence that rainforest animals have crossed an area 1000 miles wide which is now nearly all too dry for their survival, Auden (pp. 334–337) cautiously invokes cooler climate and greater relative humidity during the Pleistocene (associated with extension of Himalayan glaciers 6000 to 8000 feet lower than at the present time) which would permit greater river discharges *for an equivalent rainfall.*

Krishnan (1952, Figs. 3, 4, 5) depicts the Indian subregion as fairly well separated from the Indochinese subregion in the Eocene, Miocene, and Pliocene by an arm of the Indian Ocean piercing the continent at what is now the Ganges-Bramaputra delta and extending northeast more than 600 miles.

The hypothetical line of hills across the present Ganges-Bramaputra delta, which was an essential to early concepts of the Satpura hypothesis, could not have formed much earlier than late Pliocene, then. Auden (1949, p. 334) considered that such a hill connection was probable, but suggested too early (Miocene) an origin for it to be in accord with Krishnan's (1952) findings. Auden accepted as a probability that such a hill range did exist, at any rate, and that it reasonably could have faulted and tilted down during the Pleistocene, creating the Garo-Rajmahal Gap. Hora (1951, 1953) abandoned the concept of a former hill connection across the Garo-Rajmahal Gap (other than what escarpment the lowered sea levels of glacial maxima during the Pleistocene might have provided) without presenting better evidence for changing his point of view than for retaining it. The new opinions are interesting and possibly im-

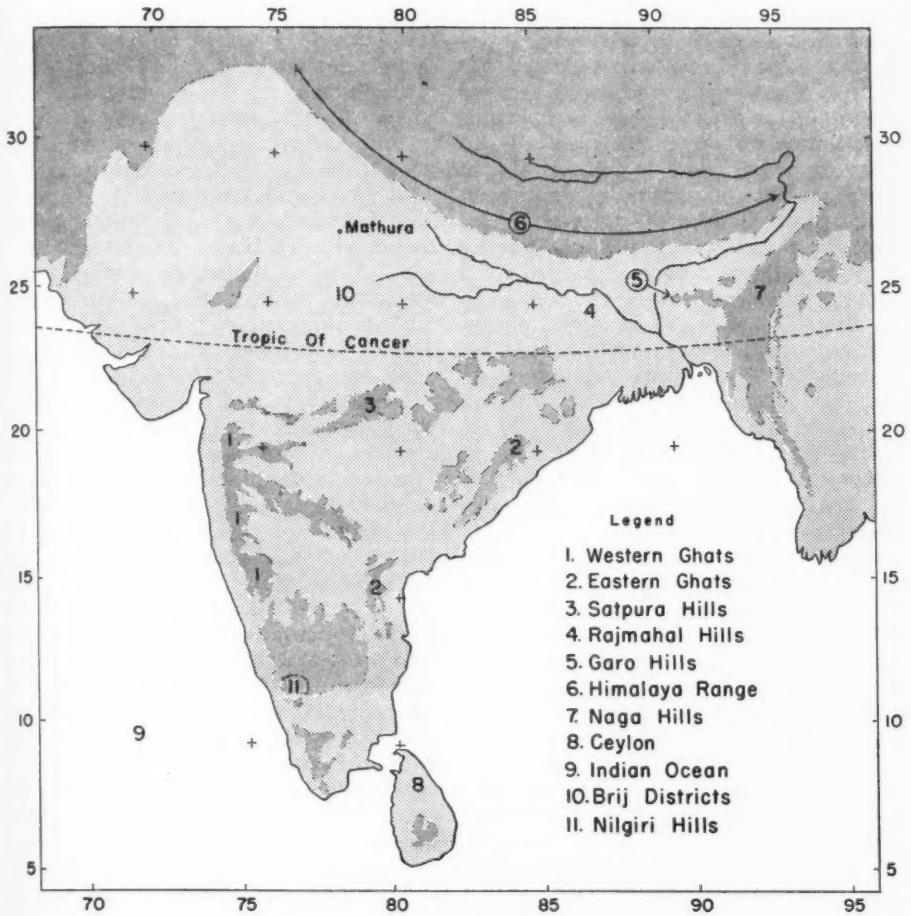

FIG. 2. The Indian subregion showing hill ranges to 1500 feet elevation.

portant, but it appears that what is needed now is impartial reporting of much well-considered new evidence, both geological and zoological. The present paper offers a few fragments of such zoological evidence which have emerged from a revisionary study of the diurnal squirrels of the region.

Continuous Range Hypothesis

Dilger (1952) has drawn attention to Randhawa's (1945) paper "Progressive desiccation of northern India in historical times" and offered an hypothesis based upon it provided with a name, the "Brij hypothesis." This hypothesis states that about 2000 years ago northern India "was covered with luxuriant evergreen tropical forests." This hypothesis is not shown to be in any significant way different from the continuous range hypothesis which Dilger correctly notes was not disposed of by Hora (1949, p. 312). The continuous range hypothesis according to Hora (loc. cit.) postulates that the places in which

the species in question is now found were once parts of its continuous range (geographical distribution), and that it has since died out in the intervening areas as a result of ecological changes there which were unfavorable to it. This concept differs from the Satpura hypothesis also in implying that the continuity was broad; former continuous range is certainly inferred by the Satpura hypothesis, but the latter hypothesis differs in conceiving a narrow corridor of continuity confined to the elevated portions of connected ranges of hills, across a thousand miles of habitat otherwise unsuited to the species in question. Since Dilger has evidently invoked Randhawa's previously existing evidence in support of an already available hypothesis, it seems conservative to use in the present paper the earlier name, continuous range hypothesis.

The evidence advanced in Randhawa's (1945) paper, together with its seductive illustrations, requires some further consideration. Sculptures of about 2000 years ago have been excavated in the area about Mathura (Muttra on some maps; about 90 miles south of Delhi) and are said to be available for reëxamination in archaeological museums in Lucknow and Mathura. The four tree species (*Anthocephalus indicus, Saraca indica, Mesua ferrea,* and *Michelia champaca*) are said to be tropical, broad-leaved evergreen trees with much higher water requirements than can be satisfied naturally in north-central India today, but all four are said to occur naturally in the evergreen rainforests of the Western Ghats and Assam, etc. The discovery in a particular locality of sculpture excellently illustrating one of these four tree species is taken as evidence that the tree depicted grew naturally in that locality. This is despite the pertinent fact Randhawa himself mentions (p. 560) that at least three of these four tree species are also cultivated. In mapping the "present day" distribution of one of the four tree species to contrast it with his evidence of former continuous range, Randhawa (1945) depends upon Hooker's 1872 "Flora of British India," supplemented only from Haines' 1921–1925 "Botany of Bihar and Orissa." Although Randhawa states that the mapped species, *Saraca indica,* the asoka, is the most hydrophytic of the four, he reasons that its greater frequency of occurrence in these sculptures indicates greater *natural* abundance of the tree in the region. Yet he cites evidence from Sanskrit literature that flowers of these trees were utilized in certain festivals of ancient India, from which one could infer that they may have had important symbolic relationship to the human forms sculptured and to the activities depicted. Randhawa was evidently so well convinced by these findings that he presents no contrary evidence intended as such for the reader to evaluate. He does mention that "elephant, horse, lion, and antelope" were the favorite animals in these sculptures. Three of the four of these inhabit fairly dry savannahs or plains, and the antelope (black buck) Randhawa himself mentions as haunting "the sandy wastes" typifying the near-desert condition of central India now. This observation is not offered as refutation of Randhawa's thesis, for the likelihood seems at least equally great that these animals are sculptured because of symbolic importance rather than natural abundance in the vicinity. The present author does not even think by the sum of these comments to disprove Randhawa's thesis, but only to point out that if anyone wishes to support the continuous range hypothesis with them, he could critically review at least the literature cited by Randhawa, check for more recent botanical explorations of relict forests in hill country of central India for additional distributional knowledge, and generally subject the evidence to sterner criticism.

Later authors in a symposium more cautiously discussing archaeological evidence relating to climatic change in the deserts of the state of Rajputana immediately

west of the Brij area, make no mention of Randhawa's paper (Ghosh, 1952; Sankalia, 1952; Vats, 1952). An existing river called the Ghaggar, with a tributary called the Markanda, flows out of the Himalayas through the Punjab States and enters the desert area in Rajputana where it runs dry. Sankalia (1952, p. 49) concludes that the climate of the region is probably becoming increasingly drier, and he seems to infer this chiefly from evidence that: 1) the Ghaggar River once extended much farther and was much larger, and 2) a considerable flora must have then been supported in the Ghaggar River area because of the quantity of kiln-burnt clay materials which included large well-burnt bricks found in mounds along the former river banks in the desert, and which would have presumably been burnt with firewood.

Tree Squirrel Distribution

The continuous range hypothesis surely requires former existence of evergreen rainforest as uninterrupted as the conjectured former continuous ranges of species that this hypothesis suggests. If such uninterrupted forest existed, it would have provided, however long it persisted, suitable habitat for tree squirrels to spread into, and the rich squirrel fauna of the Indochinese subregion would be expected to have spread into the Indian subregion by this means. This seems so axiomatic and applies with such peculiar force to tree squirrels that this segment of the mammalian fauna may possibly serve as the best available test for the applicability of the continuous range hypothesis.

The present writer (manuscript) has revisions of the genera of the tree squirrels involved (*Funambulus, Dremomys,* and *Callosciurus*) completed excepting for *Callosciurus,* and work on all but one of the species of *Callosciurus* involved is completed for this region. The distribution maps prepared in this work show collecting localities for the Indochinese and Malasian tribe Callosciurini in the forested hills of Assam and extending westward toward the Indian Peninsula via the forested finger of the Khasia Hills and Garo Hills and stopping at the Garo-Rajmahal Gap. They extend westward separately in another finger of evergreen rainforest along the face of the Himalayas into Sikkim and Nepal. The species which reach the Garo Hills *and* Nepal (or only Sikkim) are *Callosciurus* (*Tamiops*) *mcclellandi, Callosciurus erythraeus* (only Sikkim), *Callosciurus pygerythrus,* and *Dremomys lokriah.* A fifth species, *Dremomys pernyi,* reaches the main north-south ranges of Assam, Naga Hills, etc., but is so far unknown from the two fingers of rainforest projecting westward.

Some Interrelationships of Indian Species

In the Indian Peninsula there are five species of *Funambulus,* an endemic tree squirrel genus that has African affinities (Moore, 1959, p. 170). Three of these species inhabit only the rainforest region of the mountainous west coast of the peninsula and of Ceylon at its southern tip. The other two (*palmarum* and *pennanti*) are species in part adapted to more open and drier forest and together are widespread in central and northern India. *Funambulus pennanti* by the evidence of its distribution must be exceedingly well adapted to desert or near desert conditions. Although Akhtar (1958, p. 17) described *pennanti* as nesting in trees, both inside natural tree cavities and outside on crotches, and as "passing incessantly from limb to limb and tree to tree" with skill and speed, he also (op cit., p. 15) classifies it in his key as "semi-terrestrial or arboreal." The generalized observations of the behavior of *pennanti* by Krishnaswami et al (1957, p. 891) together with the above ones of Akhtar, however, leave no doubt that *pennanti* is ecologically a tree squirrel.

The distribution of *Funambulus palmarum* is nearly restricted in my records to the southern part of the peninsula, but

this species also occurs in the east-west line of hills across central India, subspecies *robertsoni* in the Satpura and other hills, and subspecies *bengalensis* in the Rajmahal Hills. It is primarily adapted to and known from the areas disturbed and inhabited by man, but C. A. Crump (*in* Wroughton, 1915, p. 108) reported *palmarum* "to be found far into the forests" as well. According to Khajuria's (1955, p. 4) ecological classification of peninsular mammals into humid, semi-humid, and desert elements, *palmarum* belongs to the humid and semi-humid elements.

If India has only recently acquired its present extreme and wide-spread aridity, something which is suggested by Khajuria's (1955) report that the existing mammalian fauna includes a desert element of only four percent, then it seems likely that the range of arid-adapted *pennanti* has recently expanded and that the range of humid-adapted *palmarum* has shrunk as the desiccation progressed. The locality records (Moore, MS.) indicate sympatry only (but rather broadly) in the range of hills across central India from the Satpuras to the Rajmahals. C. A. Crump (*in* Wroughton and Riley, 1913, pp. 53 and 54) reports these two species to be ecologically segregated in Hoshangabad where he collected 22 of *palmarum* and eight of *pennanti*. The *palmarum* is found "high up on the hills and living amongst the bamboos." *Funambulus pennanti* lives in the valleys and "differs entirely in its habits" from *palmarum*, Crump found, and he distinguished their voices. In the Rajmahal Hills, where mild physiographic relief provides fewer ecological communities, Crump (*in* Wroughton, 1915, p. 108) found the two species unsegregated. He wrote that *pennanti* is "well distributed throughout Hazaribagh where, however, it overlaps with *palmarum*, the latter, I think, predominating. At several places I shot both of these squirrels on the same ground but did not find them together in one tree." Specimens of both species are listed from four of Crump's named collecting localities. Thus, the evidence suggests that the continuous wet forest would be disadvantageous and geographically restricting to the species *F. pennanti*, whereas it is reasonably evident that continuous wet forest would enable *Funambulus palmarum* to spread, and that in its present distribution it is well poised to take advantage of such a connection by spreading into the Garo Hills or Nepal.

Mixing Across the Subregional Boundary

The distribution of *Funambulus pennanti*, although distinctly less related to evergreen rainforest than that of *F. palmarum* and thus entirely impertinent to the Satpura and continuous range hypotheses, does exhibit some points of interest relative to the barrier between the Indian and Indochinese subregions. In his ecological classification of mammals of southern and central India, Khajuria (1955, p. 3) classified *Funambulus pennanti* as "cosmopolitan," implying a considerable indifference to climatic conditions, and within its range my distributional data tend to support this concept. It may be this factor which has enabled it to reach the foothills of the Himalayas.

Although Hodgson never reported *pennanti* from Nepal during 20 years there in the early 1800's, in 1920 Baptista took a male and female at Tribini, at about 300 feet elevation on the Ganduk River where it crosses the Nepal-India border (Hinton and Fry, 1923, pp. 402 and 419). In 1947 W. N. Koelz took a female at "Hetora," Nepal (American Museum of Natural History), which is evidently Hataura (and I think even "Hetwada" of Hinton and Fry) on up the Rapti River at about 1000 feet elevation and 30 miles S.S.W. of Katmandu.

When in 1914 or 1915 Crump collected a male *pennanti* in the town of Haldibari, elevation 150 feet (Wroughton, 1916, p. 487), near the Tista River just south of Sikkim, he thought that it "Probably was introduced at Haldibari, where I saw it only in the town and not in the surround-

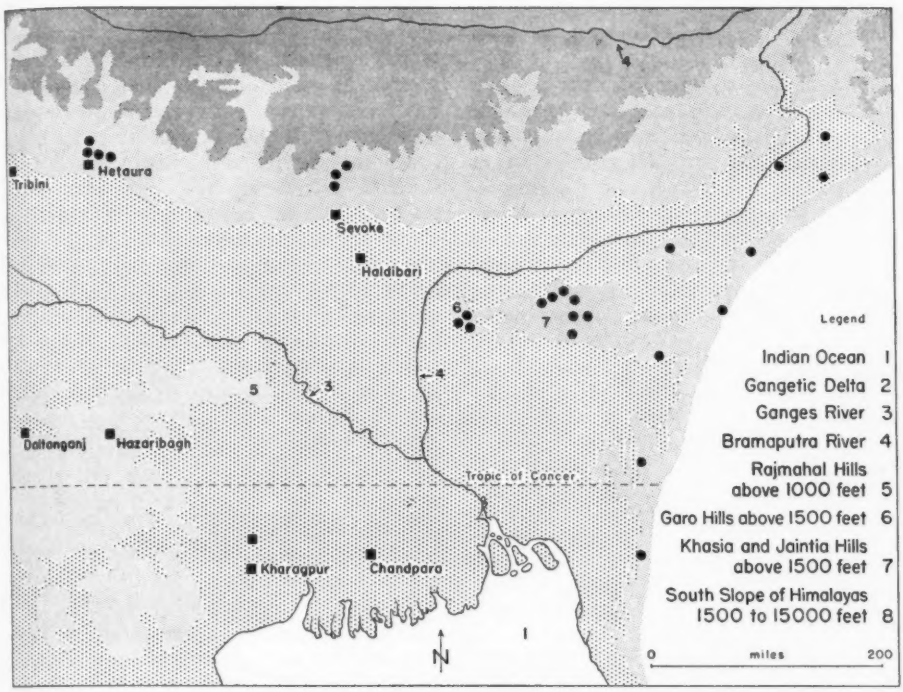

FIG. 3. Geographic relationship of the five-striped Indian squirrel, *Funambulus pennanti* (■), to squirrels of the tribe Callosciurini (●) at the boundary between the Indian and Indochinese faunal subregions.

ing villages." In 1930 H. Stevens took five specimens (Chicago Natural History Museum) of *pennanti* at Haldibari and, more significantly, one at Sevoke about 40 miles farther up the river. Thus, if this represents introduction by humans, the species is either multiple or spreading. It appears that between the Ganges Valley and the westward reaching finger of Indochinese squirrel fauna along the face of the Himalayas into the middle of Nepal, there may be a finger of Indian squirrel fauna reaching eastward at least to the Tista River.

Also interesting are recent collections of *pennanti* on the Gangetic delta, one from Kharagpur, Bengal, in 1945 by R. C. Gibbs (Museum of Zoology, University of Michigan). But most surprising of these are three (American Museum of Natural History) collected in 1947 by S. Dillon Ripley at Chandpara 40 miles east of Calcutta. This is halfway across the Gangetic delta.

If the above records of *Funambulus pennanti* do represent natural distribution (and they probably do), then this Indian squirrel taken at Tribini and Hetora [=Hataura and perhaps Hetwada] appears to overlap the range of the Indochinese tree squirrel, *Callosciurus pygerythrus lokroides,* in the valley of the Rapti River, for the latter was taken at Hetwada and Sunachir, which latter is at about 700 feet elevation and located between Hetwada and Tribini (Hinton and Fry, 1923, pp. 402, 419). The locality farther east on the Tista River where *F. pennanti* was taken, Sevoke, is on the plain at the edge of the hills, and eight miles from it into the hills at Mangpu H. Stevens collected nine specimens (Chicago Natural

History Museum) in 1930 of the Indochinese tree squirrel, *Callosciurus pygerythrus lokroides*.

It is tempting to infer from the relative collecting dates and places cited here that *F. pennanti* has been moving east and north during the past 100 years. If that were not the case, then it would seem reasonable to assume that this species has been in contact with the Indochinese tree squirrel, *C. p. lokroides*, for some time along the line separating the two faunal subregions, and that it would be equally reasonable to find *pennanti* in the delta closely adjacent to the Garo, Khasia, Jaintia, and Lushai Hills as well. It would be interesting to have more evidence on which is the case, and also on whether *pennanti* and *lokroides* must come into direct competition by occupying the same kinds of forest or whether they are ecologically segregated.

The Indian mammalogist Khajuria (letter of February 22, 1960) comments on the above problem, "I have collected in the plains around the Garo and Khasia and Jaintia Hills in Assam but did not find *Funambulus pennanti* in these areas. On the other hand, I found *Callosciurus pygerythrus lokroides* both on the hills and in the plains and even around villages and towns. In the Himalayan foothills I did not come across these two forms together but remember to have seen *F. pennanti* around towns and *C. p. lokroides* high up on the hills in these places." Thus it appears that *F. pennanti* and *C. p. lokroides* may indeed compete to the point of mutual exclusion.

Confrontation Across the Gap

Thus there is on the east side of the Garo-Rajmahal Gap, and north side of the Ganges Valley, an assemblage of four species of tree squirrels of the large tribe Callosciurini, no member of which is known to have reached the Indian subregion. On the west side of the Garo-Rajmahal Gap, and south of the Ganges Valley, there is only one species of rain-forest(?) tree squirrel, *Funambulus palmarum*, and it is of a tribe not known ever to have penetrated the Indochinese subregion. It seems obvious that if continuous forest existed between these two subregions even tenuously and for but a brief time, that under circumstances of tree squirrel distribution like the present ones, the tree squirrels of at least one subregion would spread into the other.

It is possible to speculate that tree squirrel invasions of 2000 years ago and earlier may possibly have taken place but with the result that the invaders of each subregion have since been competed out of existence by the residents. It seems to me a little doubtful, however, that four diverse species of Indochinese tree squirrels living sympatrically with each other and presumably well adjusted to habits that prevent them from coming into fatal competition with one another should, nevertheless, all four become fatalities in competition with but one Indian species.

Another possible speculation is that *Funambulus palmarum* may have a lower threshold for dry or open habitat conditions and formerly could probably reach the ranges of its eastern counterparts through continuous forest conditions suitable enough for it but too dry or scrubby for any of the species of Callosciurini to move into, and that *palmarum* then could not find, or successfully compete for, a niche among the four tree squirrel species already present. This, however, seems an excessively tenuous situation to postulate.

Confrontation of tree squirrels across the Garo-Rajmahal Gap and Ganges Valley is of members of two very distinct tribes, Funambulini on the west and Callosciurini on the east. The opposed species may, in fact, prove to possess distinction even greater than tribal (Prasad, 1957, has already proposed this) when features of the male genital tracts of Indochinese and African squirrels have been examined and made known. This evidence seems to the present author to be very strongly opposed to applicability of the continuous

range hypothesis to the time period since the latest glacial maximum.

Origin of Endemic Southern Species

There are three species of *Funambulus* which are indigenous to Ceylon and/or southern peninsular India, but since their relatives are Ethiopian rather than Indochinese or Malaysian, the Satpura hypothesis and above application of the continuous range hypothesis are not pertinent to origin of any species of *Funambulus*. Also because of their Ethiopian affinities it is not reasonable to interpret their origin as resulting from multiple serial invasions at considerable intervals from a stock conveniently located beyond some filter barrier to the north. Ripley (1949) lists 44 relict species of birds in southern India and Ceylon and in addition to these, reports nine instances of double invasions from taxa to the north, but the origin of the several species of *Funambulus* cannot be attributed to this serial invasion mechanism.

Another potential isolating mechanism by which species could have originated in this subregion would be a series of alternating periods of connection and separation between the island of Ceylon and the tip of the Indian Peninsula. A species could spread to the island during a period of connection and then, during a following period of separation, the population isolated on Ceylon might evolve so differently from the one on the peninsula, that when their ranges rejoined during the next "connection" period they should avoid both interbreeding and fatal competition.

Wadia (1953, pp. 2 and 3) attributes extraordinary stability to peninsular India indicating that excepting for some vertical faulting it has remained undisturbed "for an immense number of ages." Krishnan (1956, p. 115) generalizes, "The island of Ceylon is geologically continuous with the adjacent part of Southern India." Neither of these recent texts of Indian geology reports evidence of marine terracing in peninsular India or Ceylon. In a still more recent and more specialized work, "The Pleistocene of Ceylon," Deraniyagala (1958), p. 10) observes that within the first 100 feet of elevation, "raised" beaches occur which have an interglacial origin, and seems unconcerned with the possibility that these may be evidence of worldwide eustatic changes in the stage of the sea during the alternating growth and decay of Pleistocene continental glaciers. He does associate evidence of a submerged marine terrace at the 100 fathom isobath with the latest glacial period, and indicates that the sea level during the latest interglacial came to the 100 foot contour above present sea level.

The following account attempts to show how the present hypothetical isolating mechanism may account for the origin of four of the five species of *Funambulus*. It is necessary to assume that southern India and Ceylon were crustally stable during the Pleistocene, and that the depression by at least 90 or 100 meters below present sea level during the latest glacial period and elevation to 30 meters above present sea level during the latest interglacial period (Flint, 1957, p. 270), were approximated during each of the preceding three glacial periods and two interglacial periods.

Darlington (1957, pp. 552-553) considers interspecific competition to be a quite general and fundamental established fact. It may hardly be necessary, then, to assume that some kind of competition between very similar squirrel species does occur as a rule, and that species unsuccessful in this competition eventually become eliminated from areas where the competition takes place, even if that means extinction. It is assumed that in squirrels as Ripley (1949) believes general in the birds, first arrivals, as a first device in avoiding competition, may adapt restrictively to the rainforest leaving adaptation to deciduous forest to second arrivals. For consistency it is also assumed that each population of a species hypothetically isolated upon Ceylon would have become differentiated from

its mainland counterpart to the species level during each interglacial period. (As this produces hypothetical species which must be hypothetically lost in competition, it is of course unnecessary. It would be neater and perhaps even closer to minimum hypothesis to postulate that in these cases the isolated populations did not evolve to species level during the interglacial but remained one species. However, wastage of species by extinction seems very natural.) Another assumption is that of a separated pair of populations which have speciated through geographic isolation and then regained contact, the larger population (mainland in this case) would more often survive the ensuing competition than the smaller population.

The following eight paragraphs need to be read in reference to the above assumptions and with them will explain Figure 4.

First glacial period. (Nebraskan or Günz.) The pluvial conditions accompanying the first glacial period of the Pleistocene may have been one of the most important of the factors enabling an Ethiopian species of squirrel to spread to India. In absence of any historical knowledge of this genus from the fossil record, and for the purposes of this hypothetical treatment, the first (not intended to mean absolute first, but fourth from latest) glacial period is the logical time for the original invasion of India to have occurred. Since Ceylon would have been part of the mainland at the stage of the sea then presumed to prevail, the invading squirrel species would have occupied Ceylon as indicated in Figure 4a.

First interglacial period (Aftonian). The world-wide rise of the sea with the melting of the continental glaciers is assumed to have isolated Ceylon (Figure 4b); the isolated population and the mainland population evolve differently, becoming distinct species, nos. 1 and 2, Figure 4c.

Second glacial period (Kansan or Mindel). The original species is presumed to become more adapted to the rainforest, and the second species more adapted to the lowland and rain-shadow deciduous forests and scrub. This order of specialization for the two major ecotypes follows the pattern inferred by Ripley (1949) for birds from his own field work in this area and study of morphological and other relationships. This being a pluvial period, the rainforest spreads and, whether or not it connects, the first species attains the Ceylonese rainforest (Fig. 4d).

Second interglacial period (Yarmouth). The rainforest and deciduous forest populations on Ceylon each evolves differently from their mainland counterpart during the long isolation by eustatic ocean level of this period. Thus Ceylonese populations nos. 1 and 2 of Figure 4e differentiate to species level and are designated species nos. 3 and 4 in Figure 4f.

Third glacial period (Illinoian or Riss). Low stage of sea restores Ceylon to the mainland and permits intermixing of the two distinct rainforest species and the two deciduous forest species (Fig. 4g).

Third interglacial period (Sangamon). On the mainland where the area is far greater, the two species of deciduous forest squirrels become segregated so that they replace one another geographically, north and south (Fig. 4h). On Ceylon one of the deciduous forest species, no. 4, outcompetes the other, no. 2, and the latter becomes extinct (Fig. 4h). The two rainforest species are sufficiently differentiated in habit, however, that they become adjusted sympatrically both on the mainland and on Ceylon. During this period of isolation by high stage of the sea, the two rainforest squirrel populations and the one deciduous forest population on Ceylon differentiate to the species level (Fig. 4k).

Fourth glacial period (Wisconsin or Würm). With the isolation broken again by a low stage of the sea, the two southern species of deciduous forest squirrels, nos. 4 and 5, intermix as suggested in Figure 4m. The four species of rainforest squirrels also come into contact and to some extent into competition with each other (Fig. 4m).

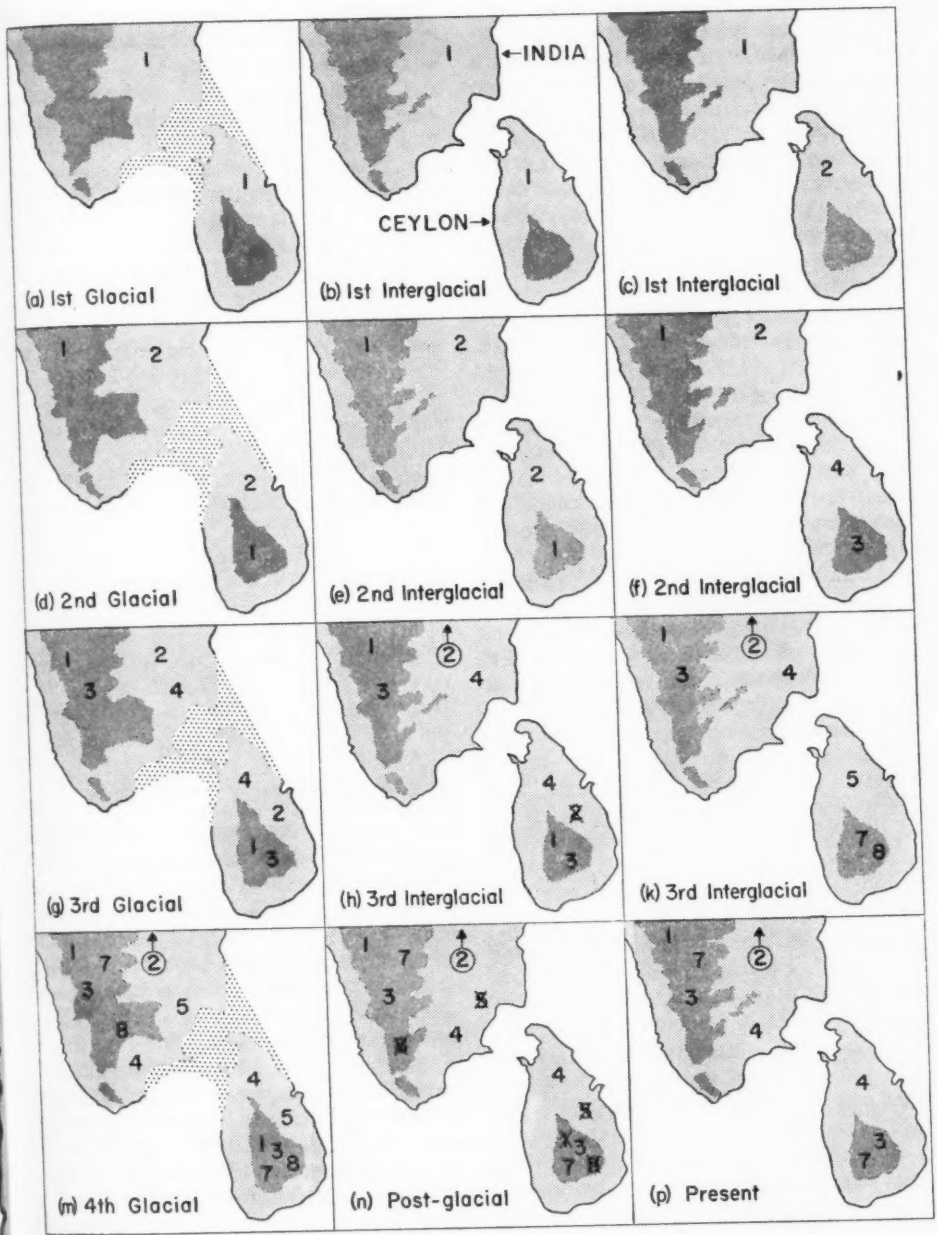

FIG. 4. Hypothetical model for origin of five species of *Funambulus* (explanation in text).

Post-glacial period. Isolation of Ceylon has been restored by eustatic rise of the sea. One deciduous forest species, no. 5, has been competed out of existence by no. 4 (Fig. 4n). One rainforest species did not manage to carry differentiation far enough to survive in a special niche on the mainland and two rainforest species failed to survive on Ceylon (Fig. 4n). The surviving five species, shown in Figure 4p, would be, according to this model, the existing five species of *Funambulus:* no. 1, *tristriatus;* no. 2, *pennanti;* no. 3, *sublineatus;* no. 4, *palmarum;* no. 7, *layardi.*

Discussion. This highly speculative and somewhat complicated mechanism nevertheless fits the following information, obtained in revising the genus. The presently existing species of *Funambulus* are five in number. Three species seem primarily adapted to the rainforest and are geographically sympatric on the mainland. The other two seem primarily adapted to open or disturbed and deciduous forest, but are largely allopatric and also differentiated in their adaptiveness to aridity. The deciduous forest seems to have fewer squirrel niches than the evergreen forest. The areally larger mainland rainforest seems to have more niches available than the island rainforest (but this may be an indication that two large populations on a large area are better able to adapt to diverse habits soon enough to enable them to avoid lethal competition with each other).

The species *layardi* "is by far the most uncommon of [diurnal] Ceylon squirrels" (Phillips, 1935, p. 237). On the mainland it is known to the present writer from only two specimens. Material of *sublineatus* from the mainland amounts to 24 specimens from 15 localities, and on Ceylon this species seems to be abundant enough for Phillips to have known it rather well. The great disparity in abundance evident in these two small squirrels of the primary jungle suggests that despite some evidence of differentiation in habits, they may be to some extent in competition. On the mainland *sublineatus* is evidently the more successful; on Ceylon *layardi* seems to have the upper hand.

No earlier explanation of the speciation of *Funambulus* in India has been offered, and the present writer (MS.) has revised the genus and found evidence for confidence in five existing species. The model, Figure 4, as interpreted in the text above suggests how four unions of Ceylon with the mainland alternating with separations, related to the four best-known Pleistocene glacial periods and their interglacials, could explain the existing number and relationships of the species of *Funambulus* in a manner not violating generally accepted concepts of zoogeography and speciation. Silas (1955) reports 2 genera, 10 species, and 10 subspecies of freshwater fishes endemic to Ceylon (p. 256). He recognizes evidence of "intermittent land connections" between Ceylon and the Indian Peninsula during the Quaternary (p. 254) and apparently thinks the isolation periods long enough for differentiation of the separated populations of clearwater river and lake fishes such as *Puntius, Labeo,* and *Esomus* to progress past the point of sexual isolation (p. 255).

Giant Squirrel Distribution

Of tree squirrels there yet remains to be considered the giant tree squirrel genus, *Ratufa.* While the giant squirrel *niche* is, I think, not pertinent to the preceding discussion of tree squirrel confrontation across the Garo-Rajmahal Gap, its *distribution* manifestly is. *Ratufa* constitutes a distinct tribe (Moore, 1959, p. 167) of somewhat uncertain relationships to the Funambulini and Callosciurini, but it occurs on both sides of the Garo-Rajmahal Gap. In revising the genus *Ratufa,* the present writer (MS.) has found no evidence of intergradation between the populations of *Ratufa* on the two sides of the Garo-Rajmahal Gap, and concludes that the two populations represent distinct species, *indica* on the west and *bicolor* on the east. They are, thus, far more closely re-

lated than *Funambulus* is to *Callosciurus* and *Dremomys,* and this fact requires some kind of an explanation such as the Satpura hypothesis and the continuous range hypothesis were intended to provide.

Ratufa indica and the Satpura Hypothesis

The distribution of *Ratufa indica* rather closely approximates that of *Funambulus palmarum,* being strongly south peninsular but including available forests across central India from the Satpuras to at least the southern edge of the Rajmahal Hills (Chaibasa, southern Bihar). Its occurrence farther south, then, down through the Eastern Ghats (see particularly Abdulali and Daniel, 1952, map) raises a question as to whether its present distribution supports the Satpura hypothesis.

The geographic distribution of characters of the subspecies seems to have a bearing on this question. Throughout its range the basic color of the species *indica* is a slightly purplish red. The form *centralis* occurring in the Satpura to Rajmahal chain of hills is characterized by black shoulders and white-tipped, black tail. The range of *R. indica centralis* extends, at least in discontinuous patches, down the Eastern Ghats (not Western) to Mysore. In the Nilgiri Hills, it intergrades with a subspecies to the south, *maxima,* which also has black shoulders and a (wholly) black tail and is distinguished by having a black rump. In the Nilgiri Hills also, *centralis* intergrades with a red subspecies of the Western Ghats to the north, *indica,* which has no black. At the very north end of the Western Ghats *indica* intergrades with a cream-colored subspecies, *dealbata,* which has no black. Although this cream-colored form is very close to the Satpura Hills, no evidence is known that it intergrades with *centralis.*

The evidence of gene flow, then, is well documented by all of what are here recognized as the intergrades, having subspecific descriptions and names (see Abdulali and Daniel, 1952). From *dealbata* southward the gene flow may be traced along the Western Ghats through subspecies *indica* into *maxima* at the south end of the peninsula. And at the area of intergradation between *indica* and *maxima* it flows (or has most recently flowed) east and north through *centralis* up the Eastern Ghats to the Satpuras and Rajmahals. This account may be followed nicely on the single map published by Abdulali and Daniel (1952, p. 472) which also illustrates all the forms in color.

The geographic arrangement of characteristics described above certainly suggests natural original spread of *Ratufa* from the vicinity of the Garo-Rajmahal Gap down the Eastern Ghats to enter the Western Ghats near the apex of the Indian Peninsula rather than spread across the Satpura Hills to the north end of the Western Ghats. While the present writer does not doubt that this geographic arrangement of color characters could have come about secondarily, it must be said that the available, existing evidence from giant squirrel distribution is contrary to the Satpura hypothesis.

Double Invasion?

The occurrence in very southern peninsular India and Ceylon of a distinctly separate species, *Ratufa macroura,* might suggest a double invasion by *Ratufa* such as Ripley (1949) reports for several species of birds. There are certain characters possessed in common by species *macroura* and *indica,* but unknown in the two species of *Ratufa* beyond the Garo-Rajmahal Gap, which bear on the double-invasion hypothesis: 1) a contrasting color mark crosses the top of the head between the ears, separating the crown from the nape. 2) a dark, narrow stripe extending from the ear down the side of the head, separating the light-colored side of the face from the still lighter colored side of the neck (very different, incidentally, from the moustachial line on species *bicolor*). These characters are evidence that *indica* and *macroura* became specifically distinct

from one another after their single common progenitor stock had crossed the Garo-Rajmahal Gap into the isolation of the Indian subregion, and become differentiated itself from the ancestral population east of the gap. From this it seems necessary, then, to infer that there has been no successful double invasion by *Ratufa* across the Garo-Rajmahal Gap. The Indian population produced by the single successful colonization has subsequently become geographically divided into two parts for so long that differentiation has proceeded past the point of sexual isolation. Possibly this differentiation took place when one population on Ceylon was isolated from the mainland for one or more interglacial periods of the Pleistocene by a higher stage of the sea. The isolated population then became the species *macroura*, that subsequently has managed to spread onto the southern part of the Indian Peninsula where it still retains a foothold, presumably by remaining restricted to deciduous forest, for near Madura Hutton (1949, p. 691) says the species *indica* [he called it *maxima*] is found in the evergreen forests of this area and not found in the deciduous forests.

The fact that the giant squirrels east and west of the Garo-Rajmahal Gap are only different at the species level, whereas ordinary squirrels differ at the tribal level, may seem to be somewhat of a mystery. When or under what circumstances might giant squirrels have crossed the gap but ordinary tree squirrels have been prevented from crossing? In contemplating this question one must also consider the virtual unanimity of published opinion that *Ratufa* occupies an ecological niche in the highest levels of primary rainforest and scarcely comes to the ground. This is a matter which has not previously been well documented, but may be done so here. Generalized field observations providing a basis for this concept of the niche of *Ratufa* are reported by Robinson or Annandale (*in* Bonhote, 1903, p. 19), Robinson and Kloss (*in* Thomas and Wroughton, 1911, p. 113), C. A. Crump (*in* Wroughton and Riley, 1913, p. 53), C. A. Crump (*in* Wroughton, 1915, p. 107), C. A. Crump (*in* Wroughton, 1916, p. 486), Phillips (1935, p. 219), Banks (1949, p. 61), Harrison and Traub (1950, p. 342), J. L. Harrison (1957, p. 420). These observations pertain to all four species of *Ratufa*. The one dissenting published observation which has reached the present author's attention is by Hutton (1949, p. 691), "Quite often I have seen these squirrels (*Ratufa indica maxima*) foraging together; one on the ground collecting nuts, etc., which the one in the tree knocks down." If this is an accurate observation, it deserves further observation and reporting in greater detail in view of its disagreement with the consensus (and also of its implying a most unusual degree of cooperation for a mammal that is reported to be not particularly social). It is not intended to question by these remarks whether the giant squirrel is ever seen specifically on the ground. S. Dillon Ripley wrote the author (January 22, 1960) of such an instance, "In 1947 I watched a *Ratufa* in southwestern Mysore on the ground running along the roadside in tropical dry deciduous forest." It is meant to point out that a question exists as to whether the oriental giant squirrels habitually come to the ground as a part of their ordinary activities.

Nevertheless, it is conceivable that population pressures reaching peaks at surely irregular and rare intervals may stimulate individuals of the genus *Ratufa* to descend to the ground at the edge of its habitat, if necessary, and strike out across large areas of unsuitable habitat. The giant squirrel reaches the climax of its great size in the vicinity of the Garo-Rjamahal Gap, for H. Stevens recorded a weight of five pounds on the labels of University of Michigan Museum of Zoology No. 35433 and Chicago Natural History Museum No. 35432 when he collected

them at Sevoke, Bengal. Both were males, but he recorded on the tag of a female from a little farther up the Tista Valley a weight of 4½ pounds. Stevens labeled five other males from this vicinity (Sevoke, Sangsir, and Tarkhola) as weighing 3 or 4 pounds, and at least one of these was an immature. A squirrel species reaching this size is physically capable, one could conjecture, of traveling considerably greater distances through unsuitable habitat (on the rare occasions when one might try) than is *Funambulus palmarum, Callosciurus* sp., or *Dremomys lokriah. Ratufa* would be subject to predation only by larger predators, which would be fewer in a given area to be crossed, than predators on ordinary tree squirrels.

Summary

On the basis of completed manuscript revisions of the diurnal squirrel genera *Funambulus, Ratufa,* and *Dremomys* and partially completed revision of *Callosciurus,* the bearing of the distribution and morphological relationships of the subfamily Sciurinae on biogeographical concepts of the Indian subregion are examined. Diurnal squirrels of only two genera extensively occupy the Indian subregion, the giant squirrels of *Ratufa* and the tree squirrels of *Funambulus.* Of the two genera only *Ratufa* ranges into the adjacent Indochinese subregion. However, one Indochinese species of *Dremomys* and three Indochinese species of *Callosciurus* range up to the subregional boundary on the east, apparently being stopped there by a conspicuous discontinuity of their forest habitat, the narrowest part of which is called the Garo-Rajmahal Gap.

Funambulus pennanti, a north Indian species which may prove to have unusually broad habitat tolerance, is shown to have (barely) crossed the subregion boundary in Nepal, to have reached it near Sikkim, and to have approached it east of Calcutta.

Apparently restricted to more moist hill habitat in central India, *Funambulus palmarum* alone in an ecological sense replaces the four species of Indochinese tree squirrels west of the most unfavorable portion of the habitat discontinuity which separates the two subregions. And only species of *Funambulus* occupy the rainforest areas farther west and south. The failure of all species of the Indochinese tree squirrel tribe to have penetrated and colonized the sparcely populated Indochinese subregion appears to invalidate application of the former continuous range hypothesis to explain rainforest restricted species now disjunctly distributed in the two regions. Thus, during the presence of the subfamily Sciurinae, it appears that the rainforest can have been broadly continuous neither across central India to Assam nor through northern India to the Himalayas and thence across to Assam, as inferred by the continuous range hypothesis. Equally, it appears that during this subfamily's occupancy rainforest cannot have extended as a narrow but continuous corridor across the Garo-Rajmahal Gap as proposed by the Satpura hypothesis.

The existing geographic distribution of morphological characteristics known now for the giant squirrel, *Ratufa indica,* witnesses against strict general application of the Satpura hypothesis to explain the route of rainforest forms from the Garo-Rajmahal Gap to the Western Ghats of southern India.

The five species of tree squirrels indigenous to peninsular India and Ceylon are presumed not to have originated as double (or multiple) serial invasions of India, and a model is presented to show how they could hypothetically have originated by differentiation in isolation (serially during the successive interglacial periods) after serial invasions of Ceylon during glacial maxima of the Pleistocene, if Ceylon and southern India were crustally stable, etc.

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Are the Pinnipedia Biphyletic?

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WHILE more primitive ancestors (creodonts, miacid carnivores) have been suggested in the older literature, respectable anatomical opinion seems to assure us that the Pinnipedia are derived from canoid (*sensu* Simpson, 1945) carnivores. This paper will support the generally discredited view that the fur seals, sea lions, and walruses, together, have a terrestrial ancestry separate from the hair seals.

The district anatomical differences between the Otariidae and Odobenidae on the one hand and the Phocidae on the other have been emphasized by some authors and belittled by others, in the light of the essentially common plan and mode of life of the Pinnipedia. There is little merit in citing anatomical differences alone as evidence of the dual origin of a taxon. The even more striking differences between the two suborders of Cetacea have in effect simply been listed (most recently by Kleinenberg, 1958) in favor of a biphyletic origin, but the argument is unfinished without evidence of suitable ancestors outside the primitive archaeocete whales.

Several authors, of whom Mivart (1885) seems to have been the first, have suggested on anatomical evidence that the otariids and walruses are derived from bear-like ancestors and the phocids from otter-like stock. Some reviewers (e.g., Kellogg, 1922; Howell, 1929, 1930; Simpson, 1945) have not felt able to exclude entirely the possibility of biphyletic origin, while others (Winge, 1941; Weber, 1904, 1928) have adamantly dismissed the notion. Simpson (1945) offers perhaps the most concise reconciliation of these otter-like and bear-like traits with the idea of monophyletic origin: "Probably the pinnipeds are an early offshot of the little differentiated late Eocene and early Oligocene canoid ancestry, paralleled by the otters, which had the same ultimate origin and a similar adaptive trend, and in other features by the bears, also with the same remote origin." It is believed, however, that some of the support for a monophyletic origin involves errors of reasoning, and that evidence has accumulated in recent years which makes a biphyletic origin from otter-like and bear-like ancestors more likely.

Anatomical Evidence from Recent Forms

Weber (1904) believed that the soft-part anatomy of pinnipeds indicated a relationship with bears. However, as pointed out by Kellogg (1922), the anatomical features used by Weber do not support his contention—being either too variable (intestinal flexures), related to body size (lobulated kidney, also in otters), simply reflecting the general or primitive carnivore condition (bicornate uterus, endotheliochorial and zonary placenta), or indicating specifically canoid rather than feloid relationships (absence of Cowper's gland).

Other soft-part anatomy seems to support a carnivore or, when specific, a canoid derivation, but does not suggest closer affinity with one or other canoid family. A reduced caecum is present in the pinniped intestine, although lost in other Canoidea except Canidae (Mitchell, 1916). Fish (1903) lists several features in common in the superficial anatomy of the brain of *Ursus* and some pinnipeds; the resemblances are somewhat less marked between the bear and the Phocidae. The "ursid lozenge" of the brain is typical of Ursidae, Mustelidae, and several pinnipeds. However, Jelgersma (cited in Mohr, 1952) studied exhaustively the microscopic and macroscopic anatomy of the

brain structure of several aquatic mammals, and concluded that *Phoca* is derivable from terrestrial carnivores without specifying what these carnivores might have been. The placental labyrinth of pinnipeds is lobulated, as in Canoidea but not Feloidea (Rau, 1925). The endothelium of the maternal capillaries is much thicker in the placenta of Mustelidae than in that of the Ursidae and Canidae (Amoroso, 1952); unfortunately there appears to be no published information on this condition in the pinniped placenta.

In spite of marked differences in the skeleton and body musculature of the Otariidae and Phocidae, each group is in its own way highly aquatically adapted, and possible anatomical links with separate living carnivores are thus obscured. One bone which cannot have been aquatically adapted is the os penis, and it is distinctly canoid rather than feloid in structure.

Differences between the skulls of Phocidae and Otariidae were the basis of Mivart's (1885) original argument in support of a biphyletic origin. Some of these differences are trivial and will not be repeated here, but the conservative basicranial region of the skull has become accepted as important in the classification of Carnivores, and this region is certainly bear-like in the Otariidae and otter-like in the Phocidae:

1) In the Phocidae and Mustelidae there is no alisphenoid canal, while in Otariidae, Odobenidae, Ursidae, Canidae, and most Procyonidae it is present.

2) The bulla of *Lutra* could easily be made to resemble that of *Phoca* by giving a rounded form to the mastoid; in both genera there is the same sort of groove between the mastoid and the tympanic. The bulla of the Otariidae, on the contrary, is very like that of the Ursidae, and the sort of groove found between the mastoid and tympanic of *Lutra* and *Phoca* is absent.

3) The mastoid process hangs ventrally considerably in the Ursidae and Otariidae, but not in Phocidae and *Lutra*.

4) In the Phocidae and Lutrinae the paroccipital and mastoid processes are not united by a ridge of bone, while in Ursidae and Otariidae they are so united.

5) More generally, the light crania of *Lutra* and the most primitive hair seals (Phocinae) have noteworthy defects in ossification of the walls. The massive skulls of Ursidae, Otariidae, and Odobenidae have few or no such defects.

Van Kampen (1905) noted these basicranial similarities, but found that ossification of the endotympanic may be involved in the bulla—as in Feloidea but not in modern Canoidea. A separate endotympanic element was described in a foetus of *Cystophora* (a highly specialized phocid genus), and a suture was noted on a bulla of a foetal sea lion, *Otaria*, apparently dividing the tympanic from the endotympanic part. The endotympanic was imputed to other pinnipeds on the basis of grooves on the bullae, often quite indistinct, although indistinct grooves are known on some canoids as well. In the pinnipeds, as in the Canoidea, there is no septum bullae, which demarcates the endotympanic and tympanic in Feloidea. Van der Klaauw (1931) states that the endotympanic of other Phocidae begins development in cartilage, as in modern Canidae, and that incipient ossification may occur in some Canidae and the badger *Meles*. It may be that ossification of the endotympanic in at least some pinnipeds is a secondary developmental approach, or due to the retention of the ossified condition known in fossil canoids. Subsequent authors vary in the amount of phylogenetic significance they attach to Van Kampen's work on pinniped bullae, but the present author believes it is unwise to dismiss the resemblances of the basicranial region to the same region in Ursidae and Mustelidae, when other anatomical evidence points to the canoid affinities of the pinnipeds.

There has been a tendency in the litera-

ture to accept the resemblances between the Otariidae and Ursidae, but not those between Phocidae and Lutrinae. The most recent relevant work of which the author is aware (Dornesco and Marcoci, 1958) is perhaps typical. They conclude that the skull of the "Pinnipedia" (by which they mean three species of hair seals) when compared in detail with the skulls of *Canis, Felis, Ursus, Meles,* and *Lutra,* most resembles the last. Faced with suggestions in the literature of derivation from undifferentiated canoid carnivores or amphicyonids, they conclude that the resemblances are convergent, produced by adaptation to aquatic life. It is difficult to understand how aquatic adaptation could thus affect the basicranial region, and it should be pointed out that the resemblances of the skull of Phocidae to that of the otter are most marked in the smaller species of the northern seal subfamily Phocinae; these same Phocinae are certainly anatomically the most primitive and *least* aquatically adapted of the living hair seals (see Laws, 1959).

On the other hand, to Winge (1941) "it hardly can be doubted that both these groups spring from the same ursid stock," and Weber (1928), who abandoned his earlier (1904) belief in ursid origins, substituted pre-ursids (perhaps amphicyonids) instead. If we examine their arguments we find that they rest on the assumption, widely held, that the Phocidae are more aquatically adapted and the Otariidae more primitive. Thus the Otariidae are presumed to resemble more closely their terrestrial ancestors and contrary characters in the Phocidae can be explained as convergent; but it must be noted that this argument involves the *a priori* assumption that the Pinnipedia are monophyletic.

The Problems of Time

One of the chief objections to a biphyletic origin has been the belief that the pinnipeds must have arisen from early undifferentiated Canoidea, antedating the origin of the ursid and lutrine lines. A recent enquiry into pinniped zoogeography (Davies, 1958) suggests that pinnipeds must have originated between middle Eocene and middle Oligocene, and favors the late Eocene as most likely.

The ages of early fossil pinnipeds have consistently been overestimated. Actually, on revisions of European stratigraphy, the earliest phocid seal (apart from unacceptable teeth or fragments) is the humerus named *Leptophoca lenis* by True (1906). This was found in the Calvert formation in Maryland, which is listed as lower middle Miocene (but may be younger, as the Helvetian, its European correlate, is now thought to be upper middle or lower upper Miocene). The earliest fossil Otariidae of the west coast of the United States, which have been listed as early Miocene by Kellogg (1922) and others since, are now best considered to be late middle Miocene (Downs, 1953).

The earliest remains are of highly differentiated seals. Several genera of Otariidae are described, and among the phocid seals all the present subfamilies are known and there is a representative of the modern subgenus *Pusa* from the Mio-Pliocene (McLaren, 1960). This early specialization has been supposed by many authors to reflect a long prior evolution. However, as Downs (1956) has pointed out, the shift from one adaptive zone (land) to another (water) is likely to be accomplished by very rapid, "quantum" evolution.

As the seals can be shown to have appeared later and to have evolved more rapidly than is generally supposed, so can suitable biphyletic ancestors be demonstrated farther back in the record.

The Mustelidae can be traced to the late Eocene. More important, aquatic mustelids, in fact the primitive otter *Potamotherium,* often formerly listed as Miocene, are known as early as Stampian or middle Oligocene. Savage (1957) believes that we must look for the beginnings of the Lutrinae in lower Oligocene.

The Ursidae are the last of the canoid families to appear. Possible bear ancestors are described from the Miocene, but undisputed bears are unknown before the Pliocene. However, it would be naive to insist upon adapted Ursidae as ancestral to the Otariidae. The Canidae seem to have resolved themselves from the dog-bear stock in the Oligocene, and bear-like traits were expressed in some forms at that time (see Hough, 1948).

Thus in summary we have something of the order of at least ten million years for the derivation of the first fossil otariids and phocids from possible separate ancestral stocks. This might be quite sufficient for the "quantum" evolution envisaged by Downs.

The Problems of Parasites

Parasites, which are sometimes more conservative than their hosts, can give valuable clues to phylogenetic history. The internal parasites of seals do not seem to give evidence of pinniped origins, perhaps because many are vectored by alternate marine hosts. The otariids and walruses have one genus of halarachnid mites and the phocids another (Newell, 1947). The anoplurid lice, however, have been suggested as having important phylogenetic significance by Hopkins (1949) and must be considered here.

The Anoplura of seals belong to the family Haematopinidae, elsewhere found only on the Canidae. Hopkins believes members of this louse family to have been parasites on the primitive carnivores. There is no need to explain their survival in pinnipeds, where mallophagan lice have become extinct, for if they were able to survive the aquatic existence they would be free from competitive extinction brought about by contact with evolved lice on terrestrial carnivores. However, the Haematopinidae from otariids, walruses, and phocids constitute a distinct group, quite different from their nearest relatives on the Canidae. Hopkins adduces this as evidence for the monophyletic origin of the Pinnipedia. It is possible that primitive lice survived true-to-type but separately in the two groups of seals, while they were modified from the primitive type on the Canidae, but a more telling argument against Hopkin's conclusions is found in his own data. The most primitive genus of lice has been found only on the northern fur seal. Another genus is confined to the southern elephant seal. A third genus, *Echinophthirus,* has been found only on seven species of northern-hemisphere hair seals. Most significantly, the fourth genus, *Antarctophthirus,* is found on five species of Otariidae, the walrus *and* the four species of Antarctic hair seals. We can only safely conclude that if *Antarctophthirus* has shown obvious cross-infestivity between otariids and phocids, then interchange of parasites was likewise possible in the past, and we cannot be sure that this peculiar group of lice was present in the ancestors of all the pinnipeds.

The Problems of Zoogeography

Davies (1958) has given the most recent and best account of the early history of the pinnipeds, presuming them to be monophyletic. However, his discussion appears to the present author to contain anachronisms and zoogeographical difficulties which can be resolved by presuming a dual origin of the pinnipeds.

Davies holds that the seals originated in the Arctic basin and have been confined to cool waters throughout their early history. The problem then is to derive two highly divergent groups from this common Arctic stock. The entire early history of the Otariidae was certainly confined to the North Pacific and the early hair seals are all found in the Atlantic-Tethyan region. Davies invokes the Bering Sea barrier, on evidence from Simpson (1947), as responsible for the divergencies in the pinniped stock. While he does not feel that movement at other times can be excluded, he concludes that "the middle Eocene, the middle to late Oligocene, and

perhaps the early Pliocene were times of exceptionally easy movement between the Arctic and the North Pacific."

Davies supposes that the break of the barrier in the middle Eocene would have been that required for the spread of the original population between Arctic and Pacific, and the subsequent closure of the barrier would allow divergence of the two forms. Present-day seals (except the tropical *Monachus* and certain otariids) are confined to waters cooler than 20°C., and Davies suggests that climatic restrictions similarly prevented early seals from venturing outside northern seas to leave their remains in presently accessible deposits until middle and late Miocene.

The later opening from middle to late Oligocene (the bridge probably did not close strongly until middle Miocene) is used by Davies to allow the ancestors of the walruses, obviously derived from otariid stock, to re-enter the Arctic seas. There they developed their special mode of life in isolation, appearing as *Prorosmarus* in the upper Miocene of eastern North America and as essentially modern walruses in the Pliocene of western Europe. An earlier suggestion by Kellogg (1922) that the walruses invaded the Atlantic by crossing submerged Central America is climatically unlikely.

There are two major difficulties with this analysis:

1) Since the development of the canoid stock (which Davies accepts as ancestors) did not occur until late Eocene and early Oligocene, it would seem that the middle Eocene is somewhat early for the Arctic origin of the pinnipeds and their movement through the Bering Strait. Although such datings cannot be taken as exact, Davies himself seems to have sensed the anachronism, for he suggests the late Eocene as the most probable time of origin elsewhere in his paper and states that his zoogeographical analysis "would necessitate a slightly earlier origin for the pinnipeds than favored by most."

2) Since to give rise to the walruses the evolved otariid stock must certainly be assumed to have entered the Arctic from the North Pacific some time between the middle Oligocene and, at the latest, middle Miocene, why did not the evolved hair seals in their turn invade the North Pacific at that time? Of course we may invoke many special arguments, but they must account for the fact that the hair seals *did* enter the Pacific from the north in the Plio-Pleistocene. It seems most logical to assume that the hair seals did not exist in the Arctic Ocean in the vicinity of the Bering Strait in the Oligocene or Miocene, although their ancestors must, on Davies' arguments, have been there earlier.

Accepting the separate geographical distributions of the earliest otariid and phocid seals, we may add further evidence that this separation was primary, and due to their biphyletic origin.

Apart from the single occurrence of *Leptophoca lenis* in eastern North America (mentioned earlier) all the earliest Phocidae are found in southern and western Europe (see Fig. 5 in McLaren, 1960). It is difficult to explain this predominance solely in terms of climate or accessibility of deposits. There seems to have been an especial favoring of the Tethyan region in the early fossil record, suggestive of an early evolutionary radiation in that area. While we must recognize the limitations of this sort of evidence, it can be pointed out that probably the earliest mustelids and certainly the earliest known otters were Palearctic.

Similarly, to match the appearance of the otariids first on the Pacific coast of the United States, we find the Oligocene elaboration of the dog-bear stock in North America (see Hough, 1948).

The Significance of Carnivore Serology

Leone and Wiens (1956) examined the serological relationships between representatives of all the families of Carnivora. They found that the reactivity of fur-seal antiserum was greater with ursid serum

than with that of any other family. Other reactions suggested the Canidae to be next closest serologically. The cross-reactivity of ursid sera was greater than that of any other canoid family, and Leone and Wiens suggest that the bears are a conservative and biochemically undifferentiated line, more representative of the early canoid stock. They conclude that the Pinnipedia are to be derived from canoid carnivores (already forecast on anatomical grounds) and that they do not deserve ordinal or even subordinal rank, but are to be included under Canoidea.

These are important results, but they have one limitation: the serological reactions of the Phocidae were not examined, for the only representative of the pinnipeds was a fur seal, *Callorhinus ursinus*. Thus we can only say that the Otariidae are most closely related to the Ursidae, and that this may indicate a direct descendence from primitive ursid stock, or may reflect a common serological conservatism from primitive dog-bear ancestors. The Mustelidae are excluded from this phylogeny, and we cannot presume that the Phocidae are involved.

Potamotherium and Semantor

Kellogg (1922) drew attention to *Potamotherium valletoni* Geoffroy, 1833, of Tertiary lacustrine deposits of Europe, which "presents many characters which may illustrate relationship with the Phocidae." The skeletal characters are of course in the direction of aquatic adaptation, but Savage (1957) in his extremely careful and thorough appraisal of the anatomy of *Potamotherium* believes the resemblances to *Phoca* to be of real phylogenetic significance. The skull of *Potamotherium* is lutrine, as the jaws and teeth are adapted to mastication. In one feature, however, the skull answers an objection offered by Mivart (1885) to his proposal of phocid-lutrine relationships: the skulls of *Lutra*, Ursidae, Otariidae, and indeed almost all carnivores, have strongly expressed postorbital processes on the frontals, but these processes are absent on the Phocidae and vestigial in *Potamotherium*.

Orlov (1933) described in great detail the hind half of a very peculiar animal discovered in late Tertiary deposits of West Siberia. It showed features of both otters and seals, and Orlov, believing that resemblances with the latter could not be convergent, named the animal *Semantor macrurus*, as the sole representative of a new family of pinnipeds, the Semantoridae. Thenius (1949) decided from the data of Orlov that of eighteen parts of the skeleton, eleven were essentially lutrine, six intermediate, and one seal-like. He then concluded that *Semantor* was no more than an aquatically highly adapted otter, and its resemblances to hair seals a result of convergence. Recently Kirpichnikov (1955) has pointed out the dangers of treating unweighted anatomical characters in this way, and has further resurrected the importance of *Semantor* by describing the humerus, perhaps from the same individual described earlier by Orlov. This humerus is very like that of the hair seals and much less like that of *Lutra* (although considerably more like the humeri of the sea otter *Enhydra* and of *Potamotherium*). To Kirpichnikov the anatomy of *Semantor* not only bespeaks a relationship with the pinnipeds, but he goes so far as to suggest that resemblances between the axial skeleton of *Semantor* and otters are superficial, and not reliable indications of phylogenetic affinity.

In view of these divergent ideas of the significance of *Semantor*, its characteristics are repeated here in a general way. There is no doubt that the axial skeleton is essentially lutrine. Except for the larger size of *Semantor*, its sacrum, pelvis, and femur are very like those of *Potamotherium*, in which, of course, Savage (1957) has shown these bones to approach the pinniped condition in several respects. The tibia and fibula are fused proximally, as in pinnipeds but not lutrines. Although the hind limb could probably be brought

forward, as in the fissipeds and Otariidae (the lesser trochanter of the femur, although reduced, was not lost as in Phocidae), the ankle approached the phocid condition in its mobility, and the foot could probably be rotated somewhat around the axis of the shank. The astragalus, although lacking the calcanear process typical of Phocidae, had lost the groove of the trochlea; this groove is well developed on fissipeds and Otariidae, but is lost in Phocidae.

In summary, one must agree with Savage (1957) that "while *Potamotherium* is a morphological link between *Lutra* and *Phoca, Semantor* is a morphological link between *Potamotherium* and *Phoca.*" Of course any such morphological series can be explained by convergence, as Thenius (1949) has done. But if we accept this as an explanation of the conformities of *Semantor* and Phocidae, then we are obliged to acknowledge the possibility of comparable convergence between the Otariidae and Phocidae. In certain critical ways *Semantor* resembles the Phocidae more than do the Otariidae, and the skeletal similarities of the two types of seals are certainly all connected with their higher degree of aquatic adaptation. *Semantor* is found in imprecisely dated deposits, but Kirpichnikov (1955) refers it to upper Miocene or lower Pliocene—too late to be directly ancestral to the hair seals. It also had at least one specialized feature, in the fusion of entocuneiform and mesocuneiform, unknown in seals or otters. Nevertheless, one must agree with Orlov that *Semantor* is a striking confirmation of Mivart's (1885) belief that the hair seals were derived from otter-like forms.

It is important to note that there is no room for the Otariidae in any relationship between the Phocidae and putative lutrine ancestors. If the otariids are related, their anatomy and serology do not suggest it. Although Howell (1930) believes that the otariid limbs in some respects show greater aquatic adaptation than the phocid, most authors give convincing evidence that the otariids are in many respects less emancipated from their terrestrial morphology. If the hair seals are derived from lutrine stock, then the Pinnipedia cannot be monophyletic.

A Speculative Account of Seal Origins

The author disclaims any originality in the preceding sections. Every suggestion made has its counterpart in the literature, and several authors have been attracted to the idea of biphyletic origins. However, it is believed that all the evidence together constitutes a more powerful argument than has hitherto been presented, and justifies a speculative enquiry beyond the limitations of present evidence.

Central Asia has been characterized since the late Mesozoic by the development of a vast freshwater system. The extent and permanence of this system has offered opportunities for aquatic evolution elsewhere matched only in the seas. The seemingly marine facies, diversity, and endemism of the fauna of Lake Baikal must owe much to this earlier and larger system, of which this great lake is one of the last vestiges (Martinson, 1958). The extensive and deep basins of the Mesozoic began to break up in the early Tertiary, but fresh water was widely persistent, and warmth-loving faunas flourished. In the late Tertiary, marine transgressions had their effect and the present fauna of the Caspian Sea derives much from that time.

It is significant that only in this part of the world was there much likelihood of development of a truly aquatic mammal. *Potamotherium* flourished in the Aquitanian lakes of the late Oligocene of France. Early Miocene orogeny destroyed the lakes and *Potamotherium,* but its relatives continued to evolve beyond the amphibious stage in the permanent lakes of Asia to the east.

Semantor must be considered an important link in the evolutionary series. The unknown skull of *Semantor* would determine finally whether this animal

should be classed as an otter or a hair seal. It was undoubtedly much more competent in the water and probably more piscivorous than present-day freshwater lutrines. It was also larger, and therefore probably more capable of swallowing its prey whole. One might predict that the teeth had lost their masticatory function and were adapted to seizing and holding fish; such secondary homodonty would surely make *Semantor* a primitive hair seal. The fate of *Semantor* was extinction by disruption of the freshwater habitat and perhaps climatic deterioration in the late Tertiary. Its relatives, the even more aquatic Phocidae, were able to take advantage of Miocene marine transgressions and invade the seas.

There are some reasons to suggest that the first true hair seals (considering the systematic position of the Semantoridae to be debatable) were inhabitants of the great inland waters of Asia. The most primitive Phocidae, the subgenera *Phoca* and *Pusa,* show a strong predilection for fresh water (the Baikal and Caspian seals and the freshwater races of the ringed and harbor seals). A freshwater origin in the Palearctic would also help explain the almost simultaneous appearance in the fossil record of southeast Europe of seals belonging to the ice-breeding northern group (Phocinae) and the tropical seals (Monachinae). We may imagine that the northern freshwater seals, perhaps by now cut off from the south, adapted to the increasing cold of the Miocene and developed the ice-breeding habit in the innermost continental reaches of the lacustrine system, or perhaps in marine transgressions from the Arctic Ocean. The ringed seal group of Lake Baikal, the Caspian and Holarctic seas moved into southeastern Europe, almost certainly from the north, at the end of the Miocene (McLaren, 1960), and is probably quite close to this primary freshwater stock. Seals in the southern part of Asia, responding to warm climates and marine transgressions, became the Monachinae of the Tethyan-Mediterranean area, whose eurythermy permitted them to cross the tropics to the Antarctic and give rise to the four related species of hair seals there, perhaps during the cooling of the late Miocene (Davies, 1958).

We cannot offer any ancestor for the otariid seals as well delineated as the ancestral Phocidae. We may presume that they were members of the same early dog-bear stock which has been suggested as ancestral to all the pinnipeds.

Davies (1958) has argued that the Pacific coast now and throughout the Tertiary with its steep, surf-battered shores and folding parallel to the coast was an inauspicious place for pinniped ancestry. In fact, as pointed out by Scheffer (1958), the North Pacific with its protected, food-rich kelp reefs is a very suitable place, and offers the sea otter as an example of more recent marine invasion. The North Pacific, where the first fossil otariids are found, was colonized not from another ocean but from its own shores, probably from northwest North America in the Oligocene.

When the Phocidae entered the sea they were already highly adapted lacustrine carnivores, as sleek and efficient as we know them today. It is perhaps significant that the otters are inclined to be fossorial. Savage (1957) indicates that even in *Potamotherium* the forelimb may have been used in digging. (Are the primitive ringed and Baikal seals merely preadapted to digging out their birth lairs in the snow on the ice, or were the ancestral Phocidae fossorial?) Thus the Lutrinae and by inheritance the Phocidae have concentrated on the hind limb as an organ of propulsion.

The Otariidae, on the other hand, entered the sea across the northwest coast after a history as littoral carnivores. Their evolution was rapid and their aquatic adaptation very thorough, but still a modification of a terrestrial morphology rather than an improvement on an already established aquatic morphology. The otariids

have concentrated on developing the forelimb—a great improvement on the primitive "dog-paddle." Most otariids spend much time on land in large social units, and retain much more terrestrial competence than the Phocidae. This was permissible among the skerries and reefs of the North Pacific, with the freedom from terrestrial predation. The more primitive Phocidae tend to avoid the land (the ringed seal almost never comes out on land in the ice-free summer, and the harbor seal is a wary animal of inaccessible banks and skerries). Extremes of sociality and the tendency to spend much time on land have developed among the higher Phocidae (see Laws, 1959). Both the land habit and gregariousness were unsuitable in inland lakes and seas, with the danger from terrestrial predation.

We will not conclude by offering a taxonomic revision of the pinnipeds as a group of biphyletic origin. It is believed that the burden of proof now lies with those who assume a monophyletic origin. Before we can speak with any finality, more fossil evidence will be required. As a final statement the author would like to plead that the entire carnivore series be examined again serologically, this time including both phocid and otariid seals in the analysis.

Summary

1. Anatomical evidence suggests that pinnipeds are derived from canoid carnivores. Mivart (1885) was first to point out that the conservative basicranial regions support a derivation of Otariidae (and Odobenidae) from bear-like and Phocidae from otter-like ancestors. Possible differences from modern canoids in the development of the pinniped bulla do not appear to discredit these relationships. There has been a tendency to accept the connection of Otariidae with Ursidae, or pre-ursids, and to reject the phocid-lutrine resemblances as convergent, but the reasons for this seem invalid.

2. It has been objected that the pinnipeds must have appeared before the evolution of the ursid and lutrine lines of carnivores. The first fossil Phocidae appear in lower middle and the first Otariidae in upper middle Miocene. The Lutrinae probably originated in early Oligocene and suitable otariid ancestors could be found among the dog-bear stocks of that time. Aquatic mammals can be expected to develop by "quantum" evolution, and at least ten million years are available for the biphyletic evolution of pinnipeds before their appearance as fossils.

3. The anoplurid lice of Pinnipedia have been used to support a monophyletic origin, but the argument is shown to be untenable.

4. The paleozoogeography of pinnipeds indicates that the Otariidae developed in the North Pacific and the Phocidae in the Palearctic, and that their early geographical separation was primary, and due to separate origins.

5. Serological study of the carnivores has been taken as added evidence that the pinnipeds are closely related to Ursidae and probably derived from undifferentiated Canoidea; however, only an otariid seal represented the Pinnipedia in this study.

6. The late Oligocene otter *Potamotherium* has many anatomical foreshadowings of the Phocidae. Orlov (1933) described *Semantor macrurus* from the late Tertiary of West Siberia as representing a new family of Pinnipedia. The axial skeleton is essentially lutrine, the hind limbs and girdle intermediate, and the hind pes and humerus are markedly phocid-like. Such adaptations to aquatic life can always be dismissed as convergent, and the systematic position of *Semantor*—whether otter or seal—has been debated, but there appears little doubt that *Semantor* is a valid morphological link and may be a descendent of the primitive hair seal ancestors.

7. It is suggested that the Phocidae arose from lutrine ancestors in the extensive and permanent lacustrine systems of

Tertiary Asia, and that they invaded the seas through marine transgressions in the Miocene. The Otariidae may have developed from littoral canoid carnivores of the northwest coast of North America. These separate origins seem to account for certain fundamentally divergent anatomical and behavioral traits in the two kinds of seals.

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Competition and Evolution in Cave Crayfishes of Southern Indiana

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TWO species of crayfish are common in the caves of southern Indiana, often coexisting in the same cave (Eberly, 1954, 1955). *Orconectes pellucidus* (a somewhat variable species with several subspecies already designated by various workers) is the famous blind white cave crayfish found originally in Mammoth Cave. The other species is a form of *Cambarus bartoni* which has up to the present been identified as *C. bartoni laevis*.

Both of these species are ecological equivalents, and when they occur in the same cave come into direct competition with each other. The main environmental factor involved in this competition is food which is naturally scarce in caves. The chief food seems to be slow-moving isopods of the genus *Caecidotea*. However, *C. bartoni*, being much larger and more powerful, can and occasionally does kill and eat the other crayfish and is even cannibalistic at times.

In this intense but slow-moving drama of the survival of the fittest, only one species seems destined to survive. Food is too scarce to permit both species to maintain very large populations side by side. The outcome will depend on the degree of specialization or adaptation to the cave environment.

The usual cave adaptations are well known. The characters most relevant to this discussion are the following:

a. White or bleached color.
b. Long, slender body.
c. Eyes hypertrophied or completely lacking.
d. Highly developed sensory organ systems, including longer antennae, increased setation, highly branched setae, etc.
e. Physiological adaptation to the scarce food supply.

Two things seem to suggest that *Orconectes pellucidus* has been an inhabitant of caves for a long time. In the first place it shows these cave adaptations developed to a high degree. The body is colorless and transparent (pellucid) and the eyes are completely functionless, showing a complete absence of facets, cornea, rods and cones as well as the pigment layers normally present (Packard, 1888). Sensory setae abound over much of the body surface, especially on the antennae, antennal scales, and uropods. These setae tend to be branched, feather-like structures, longer than setae of above-ground crayfish. Body size as illustrated by the weight/length ratio gives figures usually less than 0.040. Adaptation to scarce food supply is illustrated chiefly in the rate of oxygen consumption. It has been noted by several workers that cave crayfish survived longer in sealed jars than surface crayfish. In other words, a given supply of oxygen will last the cave crayfish longer. This lowered rate of metabolism is interpreted as meaning that lower energy demands of the crayfish (accompanied by less activity) make a given amount of food "go further." This will be considered later in comparison with the other species of crayfish. All in all, *O. pellucidus* may be considered a typical, well-adapted cave animal.

A second observation indicates the antiquity of *O. pellucidus*. There is little doubt now that cave animals are descended from normal above-ground ancestors. It is difficult to relate *O. pellucidus* to any epigean species now living in that area. Some consider *O. affinis* to be its

closest relative, but this species does not occur in the Indiana-Kentucky cave area. Ortmann (1931) thinks *O. sloanei* and *O. indianensis* are the remnants of the surface stock from which *O. pellucidus* was derived, but modern workers have disagreed. Hobbs (1948) suggests that the *O. pellucidus* complex might even form a natural group, without any close relatives.

This absence of a closely related surface population from which the cave forms could have been derived can be explained in two ways. Either *O. pellucidus* has been in the caves a long time during which the surface race has become further diversified, modifying considerably the ancestral characters, while the cave forms have been relatively unchanged in those characters now considered taxonomically important, or the cave forms themselves have departed from the ancestral types after becoming isolated in the caves.

If the latter alternative were the case, one might expect the crayfish of the different cave systems to differ among themselves at least as significantly as the various surface populations within the same area, since the cave populations are isolated from each other as well as from the surface crayfish stock. There is, however, a surprising homogeneity among the different populations of *O. pellucidus*. So far, five different forms have been designated, including *O. inermis* from southeastern Indiana; *O. pellucidus testii* from Monroe County in Indiana; *O. pellucidus pellucidus* from southern Indiana and northern Kentucky; *O. pellucidus packardi* from southeastern Kentucky; and *O. pellucidus australis* from northern Alabama.

The writer is of the opinion that all of these cave crayfish in the Indiana-Kentucky-Alabama cave region are descended from a once wide-spread surface population that was relatively undifferentiated at that time. After entering the cave, the cave adaptations mentioned earlier developed while certain features which are now used in taxonomic determinations, e.g., the form of the male genitalia, remained relatively unchanged. There are, of course, slight variations among the various populations of *O. pellucidus*, but not as much as in the above-ground stock which proliferated many different species and varieties. Faxon (1885) was one of the first to point out the primitive nature of the characters of *O. pellucidus*.

All of this seems to suggest that certain characters which are readily modified and diversified in terrestrial populations at least change at a much slower rate in cave environments and are perhaps subject to a narrower range of variation, while other characters may react just the reverse. Certainly many features of the epigean environment that may influence natural selection are absent from the cave while a whole new set of environment pressures comes into play.

The other crayfish, *Cambarus bartoni laevis*, presents a slightly different picture. Many early writers supposed it was merely a transient, having entered the cave accidentally and temporarily. It is apparent now that it is a true cave dweller. It is, in a sense, an intruder into the domain that once was ruled by *Orconectes pellucidus*. This is the origin of the competition referred to earlier.

Cambarus bartoni laevis is probably a very recent introduction into the caves. This is indicated by several considerations. In the first place, its ancestral stock is very much in evidence in surface streams of southern Indiana. In fact, taxonomists still use the same name for both. There are, however, several ways in which the two forms are differentiated that lead me to think we have here a new cave species developing, becoming morphologically distinct from its surface ancestors.

The color of the cave *bartoni* is lighter than that of its surface relatives. There is a marked reduction in the size of the eyes as well as an increase in the relative length of the antennae. Banta (1907) found the antennae of surface forms aver-

aged about 92% of the body length while those from Mayfield's Cave were over 104% of the body length. The body of cave *bartoni* is much longer than that of surface animals, whereas the weight per unit length is less. These differences are consistent and rather uniform in cave *bartoni* from several locations in southern Indiana. In these and other respects the cave *bartoni* seem intermediate between the surface *bartoni* and *O. pellucidus*.

Secondly, the idea that the cave *bartoni* is a recent introduction is in harmony with the theory of Ortmann (1905) regarding the origin and dispersion of the different groups of crayfish. According to him, the genus *Orconectes* arose in the area near southern Indiana, Illinois, northern Kentucky, etc., and spread out in all directions from here. The genus *Cambarus* on the other hand had its origin farther south and west. It followed a migration route southeastward, then northward along the Allegheny Mountains, and westward again along the Ohio River. By the time *Cambarus* had reached southern Indiana, *Orconectes* had become well established in the caves of that part of the country. Also by this time *Cambarus* had differentiated into many species and varieties. The *Cambarus* of Mammoth Cave (*C. bartoni tenebrosus*) is from a different surface stock than the *Cambarus* of southern Indiana. Members of the genus *Cambarus* that entered caves in southern Missouri, Alabama, Tennessee, and Florida much earlier show more advanced cave characteristics than those of Indiana and Kentucky. Altogether, six species and two subspecies of cavernicolous *Cambarus* have been described.

In other ways it can be seen that *bartoni* is not so well adapted to cave life as *pellucidus*. Interesting data are obtained by comparing the oxygen consumption of the two species. Oxygen consumption per gram of weight is higher in *pellucidus* but since *bartoni* is heavier, the consumption per animal is greater in the latter species. The parameter W/L might serve as a good index of ecological size. If the oxygen consumption per hour is divided by the ecological size, an index (Q_m) is derived which seems to indicate degree of adaptation of metabolic rate to an environment low in food. This is, of course, an extremely tentative suggestion, since there are insufficient data at hand yet to tell if this represents a real relationship. It can be illustrated by the following data from four animals:

SPECIES	W	L	W/L	Q_m
Orconectes pellucidus, m	1.5 g	42.2 mm	0.033	3.64
Orconectes pellucidus, f	1.8 g	46.1 mm	0.039	2.61
Cambarus bartoni laevis, m	4.5 g	52.7 mm	0.085	1.47
Cambarus bartoni laevis, m	21.1 g	82.8 mm	0.255	1.19

Unfortunately, no such data are available for surface *bartoni*. It is apparent, though, that the cave *bartoni* need more food per animal for survival than does *pellucidus*. When food is especially scarce, *bartoni* would either kill and eat *pellucidus* or die. I have several times seen large *bartoni* dead in a pool for no apparent reason except perhaps starvation. At these times, no other animals which might have served as food were seen.

And so, if *C. bartoni laevis* can continue to survive in the caves, it will likely become better adapted to the cave environment than it is now. As it becomes better adapted, it will be more successful in its competition with *O. pellucidus*. Only the future holds the answer to the outcome of this struggle. But even now several possibilities are clear. The most obvious conclusion is that *pellucidus* may eventually be exterminated by the larger and more powerful *Cambarus*. (Is that the reason for the absence of *Orconectes* in the caves of Tennessee inhabited by the very successful cave-adapted *Cambarus hamulatus*?) This is not the only choice that

presents itself. A small cave crayfish in Florida, perhaps faced with the same situation, adapted itself to the ceiling of submerged passageways in the caves while the larger species lived "right-side-up" on the bottom in the usual crayfish manner (Hobbs 1942). If *C. bartoni laevis* becomes too aggressive, *pellucidus* may try something like that. It may still be that reduced populations of both species can continue to live in the caves. It may also be that as *bartoni* becomes better adapted to caves, *pellucidus* will become even better adapted than it is now, continuing to stay ahead of its competitor. Whatever the outcome, I am sure of only one thing: none of us will be around to see it.

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A Terrestrial Flatworm Well Established Outdoors in the Northeastern United States

ALEXANDER B. KLOTS

ALTHOUGH terrestrial flatworms have long been known to exist in many parts of the world, especially in tropical and subtropical regions, these extremely interesting animals have been studied mainly by taxonomic specialists and are little more than names to a great many biologists. The majority of the described species are known only from a single finding or from a scattering of records. The best known are those which, like *Bipalium kewense* Moseley, 1878, have been widely spread by man's horticultural activities, are common in greenhouses and conservatories in temperate zones, and have succeeded in establishing themselves outdoors in warmer regions. Relatively few are able to persist outdoors in regions subject to lengthy soil-freezing.

In eastern North America, *Microplana atrocyaneus* (Walton, 1912), is known from Illinois, Missouri, and Arkansas, eastward into Virginia, New York, and North Carolina; *Microplana rufocephalata* Hyman, 1954, has not been refound since the original finding at 2600 feet elevation in Harlan County, Kentucky; *Diporodemus indigenus* Hyman, 1943, has been recorded from various elevations to 6000 feet from Kentucky and Tennessee, possibly Michigan, eastward into Atlantic coastal states from North Carolina to New York; and *Rhynchodemus sylvaticus* (Leidy, 1851), formerly known only from Ohio, Pennsylvania, and Rhode Island, was rediscovered outdoors in recent years by Ogren (1955, 1957) in Illinois, Wisconsin, and New York. These four species are presumably Appalachian endemics although the endemicity of *Rhynchodemus sylvaticus* is open to question. Further, the imported *Bipalium kewense* is now established outdoors in the Gulf States and the Atlantic Coastal Plain to at least North Carolina (Hyman, 1943, 1954); and another imported tropical land planarian, *Dolichoplana striata,* is flourishing outdoors in Florida (Hyman, 1954).

Bipalium adventitium was named by Hyman in 1943 from a single specimen from Pasadena, California, and is now known to be common in California. It was next found, by Dr. Hyman herself, in 1947 in gardens at Millwood, Westchester County, New York, when about ten specimens and two egg capsules were seen. One or two specimens have since been seen almost annually in the Millwood area. Then, in 1955, specimens of this species began to turn up in student collections and during field trips of the field zoology and animal ecology course of the City College of New York taught by the writer. In 1955 three specimens were recorded from New Rochelle, Westchester County, New York, and Pelham Bay Park, New York City. Every year since then a dozen or more specimens have been taken in Pelham Bay Park and in the town of Pelham itself; and many more have been observed but not collected. The species is obviously widely distributed in this southeastern part of Westchester County, since specimens have even been taken under boards and flat stones on the edge of a lawn in a thickly populated area in North Pelham. Most, however, have been found under stones and dead wood in rich, mesic woodland, in the burrows of the earthworms on which they feed. No diminution

in numbers was noticeable in the autumn of 1959, despite the severity for soil-inhabiting organisms of the winter of 1958–1959.

The largest mature specimens seen have measured about 60 mm. in length by 3–4 mm. in width when extended. The head has the typical lunate or meat-chopper shape characteristic of the genus *Bipalium*. The color in life is a rather bright orange brown with a single, narrow, distinct dark middorsal line. The species can hardly be confused with anything else known from the area. It appears to be quite hardy in captivity, for specimens have been kept for several months in small jars of moist earth, where they feed freely on small annelids; they also eat slugs, insect larvae, and the like. Attention is called to the suitability and value of this flatworm as demonstration material in biology teaching, also as an experimental animal.

Some further records have been provided by Dr. Hyman. A single specimen, sent for identification by the United States National Museum, was collected by P. W. Davis at Port Washington, Long Island, New York, in an earthworm burrow under flagstones on October 8, 1958. Dr. W. C. Grant, Jr., reported the taking in Denison Park, Williamstown, Massachusetts, in April and May, 1960, of about 20 specimens ranging in length from 8 to 50 mm. They were found under the bases of tree trunks, in litter of partially decomposed pine needles and loose humus in association with earthworms, sowbugs, and millipedes. None were found elsewhere in the region. S. Polivanov brought for identification one worm taken under a piece of bark at Nevis, New York, about 20 miles north of New York City.

It is evident that *Bipalium adventitium* is spreading in the northeastern United States and may be expected to occur in almost any piece of mesophytic woodland. The species is remarkable among imported tropical land planarians in its ability to withstand severe winters and to breed sexually in the north temperate zone.

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Unrecorded Papers of Rafinesque and Jacob Green

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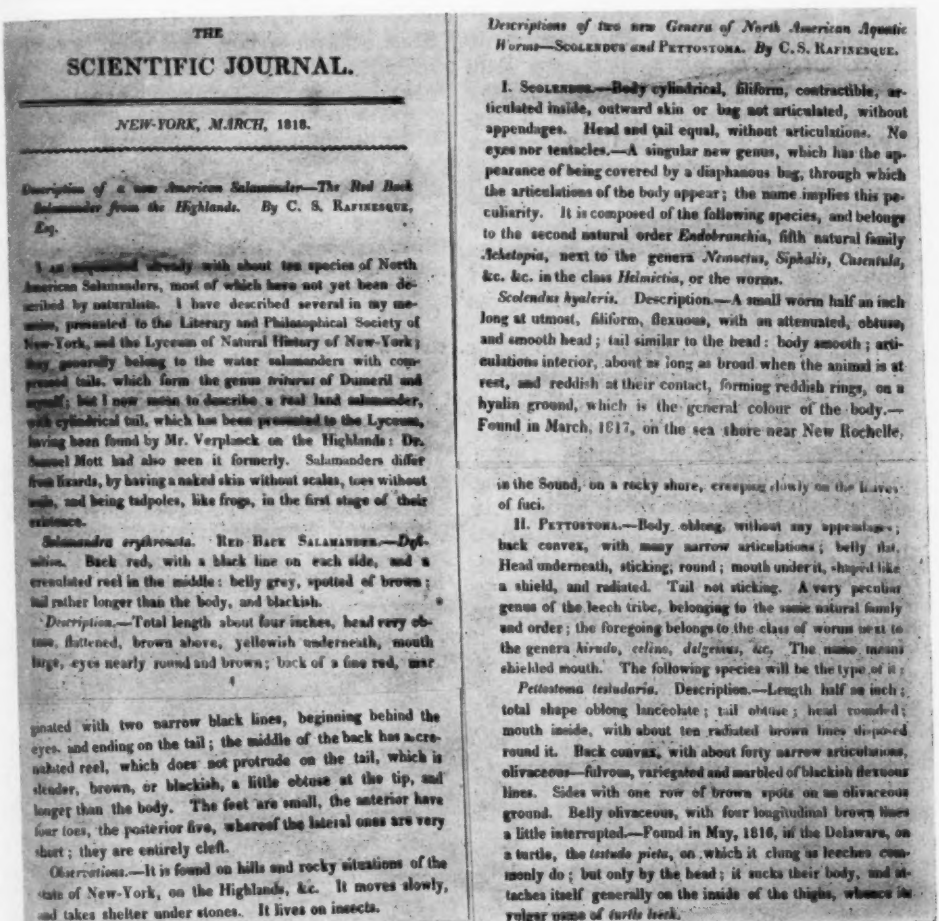
THE *Scientific Journal,* an obscure American periodical devoted primarily to mathematics, published ten issues during its short existence. The second number, dated March, 1818, contained two short papers (herein reproduced) by Constantine Samuel Rafinesque in which he described two genera of aquatic worms, *Scolendus,* type species *S. hyaleris,* and *Pettostoma,* type species *P. testudaria,* and a new species of salamander, *Salamandra erythronota.* The seventh number, dated August, 1818, contained an article by Jacob Green on leeches, in which he pro-



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Description of a new American Salamander—The Red Back Salamander from the Highlands. By C. S. RAFINESQUE, Esq.

I am acquainted already with about ten species of North American Salamanders, most of which have not yet been described by naturalists. I have described several in my memoirs, presented to the Literary and Philosophical Society of New-York, and the Lyceum of Natural History of New-York; they generally belong to the water salamanders with compressed tails, which form the genus *triturus* of Dumeril and myself; but I now mean to describe a real land salamander, with cylindrical tail, which has been presented to the Lyceum, having been found by Mr. Verplanck on the Highlands: Dr. Samuel Mott had also seen it formerly. Salamanders differ from lizards, by having a naked skin without scales, toes without nails, and being tadpoles, like frogs, in the first stage of their existence.

Salamandra erythronota. RED BACK SALAMANDER.—*Definition.* Back red, with a black line on each side, and a crenulated reel in the middle: belly grey, spotted of brown; tail rather longer than the body, and blackish.

Description.—Total length about four inches, head very obtuse, flattened, brown above, yellowish underneath, mouth large, eyes nearly round and brown; back of a fine red, mar-

gnated with two narrow black lines, beginning behind the eyes, and ending on the tail; the middle of the back has a crenulated reel, which does not protrude on the tail, which is slender, brown, or blackish, a little obtuse at the tip, and longer than the body. The feet are small, the anterior have four toes, the posterior five, whereof the lateral ones are very short; they are entirely cleft.

Observations.—It is found on hills and rocky situations of the state of New-York, on the Highlands, &c. It moves slowly, and takes shelter under stones. It lives on insects.

Descriptions of two new Genera of North American Aquatic Worms—SCOLENDUS and PETTOSTOMA. By C. S. RAFINESQUE.

I. SCOLENDUS.—Body cylindrical, filiform, contractible, articulated inside, outward skin or bag not articulated, without appendages. Head and tail equal, without articulations. No eyes nor tentacles.—A singular new genus, which has the appearance of being covered by a diaphanous bag, through which the articulations of the body appear; the name implies this peculiarity. It is composed of the following species, and belongs to the second natural order *Endobranchia,* fifth natural family *Ichtiopia,* next to the genera *Nemertus, Siphalis, Caecutula,* &c. &c. in the class *Helmictia,* or the worms.

Scolendus hyaleris. Description.—A small worm half an inch long at utmost, filiform, flexuous, with an attenuated, obtuse, and smooth head; tail similar to the head: body smooth; articulations interior, about as long as broad when the animal is at rest, and reddish at their contact, forming reddish rings, on a hyalin ground, which is the general colour of the body.—Found in March, 1817, on the sea shore near New Rochelle,

in the Sound, on a rocky shore, creeping slowly on the leaves of fuci.

II. PETTOSTOMA.—Body oblong, without any appendages; back convex, with many narrow articulations; belly flat. Head underneath, sticking, round; mouth under it, shaped like a shield, and radiated. Tail not sticking. A very peculiar genus of the leech tribe, belonging to the same natural family and order; the foregoing belongs to the class of worms next to the genera *hirudo, celine, dalgetus, &c.* The name means shielded mouth. The following species will be the type of it;

Pettostoma testudaria. Description.—Length half an inch; total shape oblong lanceolate; tail obtuse; head rounded; mouth inside, with about ten radiated brown lines disposed round it. Back convex, with about forty narrow articulations, olivaceous—fulvous, variegated and marbled of blackish flexuous lines. Sides with one row of brown spots on an olivaceous ground. Belly olivaceous, with four longitudinal brown lines a little interrupted.—Found in May, 1816, in the Delaware, on a turtle, the *testudo picta,* on which it clung as leeches commonly do; but only by the head; it sucks their body, and attaches itself generally on the inside of the thighs, whence its vulgar name of *turtle leech.*

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posed two specific names, *Hirudo testudaria* and *H. multevora*. A search of the journal disclosed no other papers of interest to zoologists.

Zoological bibliography apparently has never recorded these papers. Meisel (1924–29) failed to list any of the articles and the two by Rafinesque have not been noted by Fitzpatrick (1911) in his excellent bibliography. Rafinesque's generic names do not appear in Neave or other zoological nomenclators, and as far as can be determined Green's proposed names are not to be found in existing *Hirudo* literature.

An interesting note concerns *S. erythronota* Rafinesque, and curiously enough involves Green (1818), who in describing a species of salamander gave Rafinesque's name to it, explaining "I have given Mr. Rafinesque's name of a species found in rocky situations in New York to this, believing them to be only varieties." It is evident that Green had knowledge of Rafinesque's article, for the lead sentence in his article on leeches begins: "Mr. Rafinesque, in the 2d No. of your Journal . . ." Green's article was read before the Academy of Natural Sciences of Philadelphia on May 12, 1818, and the signature comprising his article in the Academy's *Journal* is dated Sept. 1818. Bishop (1941) and others have credited *erythronota* to Green. Harlan (1827) seems to have been the only author willing to give Rafinesque some credit for naming this species. He cites: *S. erythronota* Raf. Green. *Journ. Acad. Nat. Sc.* vol. I, p. 356. Obviously, the specific name *erythronota* is to be credited to Rafinesque, rather than to Green, as is usually done.

The copy of the *Scientific Journal* used in preparing this paper was obtained from Yale University Library on interlibrary loan. The *Union List of Serials* notes the holdings of other libraries under the headings (1) *Monthly Scientific Journal* and (2) *Scientific Journal*. The double entry results from one library listing its holdings under the cover-title while all other libraries have noted holdings on the basis of the caption-title. The introductory address of the editor, W. Marrat, "On ushering the first number of the *Scientific Journal* into the world . . ." clearly shows his intent regarding a title.

The journal is available on microfilm as a part of the American Periodical Series: 1800–1850, produced by University Microfilms of Ann Arbor, Michigan. Reel 239 includes all papers mentioned; reel 146 contains only the Rafinesque articles.

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Points of View

Some Reflections on Phylogenetic and Typological Taxonomy

Introduction

With S. G. Kiriakoff (1959), I agree that several recent attempts to define a "phylogenetic" *versus* a "typological" method in systematics have not been impressive and have introduced considerable philosophical confusion, although I do not agree that the European group alone has the key to phylogenetic taxonomy. Biologists are usually not good philosophers, and European biologists have been in advance of most of their American colleagues in this regard. The failure of biologists, especially in this country, to think or speak clearly about exactly *what* they are doing, in philosophical terms, is evident. It also is one of the several reasons why American biologists have been surpassed, in both respect and rewards, by their colleagues in the physical sciences.

It is quite true that a good deal of what American systematists have been calling phylogenetic taxonomy is to be labelled typology. This seeming error is as clearly evident in my own paper on the subject (Myers, 1952) as it is in many others. However, the distinction in viewpoint between the type of systematics which I was espousing and the negation of any immediate consideration of phylogeny in building a classification, which was inherent in the method I was criticizing, is not small. Moreover, I do not believe that Kiriakoff's methodology is beyond criticism.

Different Problems, Different Views

One fact that has not always been fully recognized, either in Europe or America, is that the thinking done by a systematist is profoundly influenced by the state of knowledge of the group of organisms on which he specializes, as well as by the very nature of that group. While different systematic specialists may now be able to agree fairly well on the processes of speciation, their thinking about the systematics of higher taxa is likely to be poles apart. For example the mammalogist generally knows considerable about the general anatomy of most of the organ systems of the living members of his group, but he derives his major classification chiefly from the abundant fossil record of at least one complex organ system—the skeleton.

The ichthyologist, on the contrary, has a vastly larger living group to deal with (33,000 fish versus perhaps 4,000 living species of mammals), yet the anatomy of most included families is almost a blank, and the fossil record is, for a class so large, excessively scanty. There is the greatest diversity of opinion even in regard to the ordinal classification of most recent bony fishes. Under such conditions, when anatomical study shows that a series of families possesses one pattern of, let us say, an important nerve-complex, and another series a different one, and the differences and similarities in other characters are not in conflict with this finding, or tend to support it, my belief is that we are uncovering phylogenetic relationships, however typological the approach may be.

In insects, a still different situation is found. The insect orders, despite the enormous size and diversity of the group, appear to be relatively stereotyped. Few entomologists know much about anything but the external morphology of their insects or take any interest in improving the classification by deeper anatomical study. Few of them have had the rewarding experience of seeing their fixed ideas

on the limits and relationships of higher groupings upset by anatomical or paleontological research.

As a result, if systematists of the three fields mentioned were asked (*in vacuo*, so to speak) to draw up tenets of systematics, I suspect that the results would be widely different, as well as classifiable, on the whole, by conditions in the three representative fields.

In a different way, the problems faced by botanists differ in several respects from those of zoologists. Plant anatomy is simpler than animal anatomy, and is probably a less sure guide to phylogeny. In general botanists have lagged behind zoologists in anatomical studies. Botanists have a greater tendency, and more reason, to believe in reticulate evolution and to accept probable cases of the polyphyletic origin of higher taxa. In plants, the "continuity of the germ plasm" (Weissmannism) means little, in animals much. And the mere fact that most plants are stationary inevitably also affects botanical thinking in evolution and taxonomy.

Finally, and perhaps most important, the systematist engaged in perfecting the detailed knowledge of a local well known flora or fauna, especially if it is as relatively impoverished and well studied as the fauna and flora of Northwestern Europe, is likely to view all systematic problems in a very different light than a worker on the interrelationships of the members of a large and poorly known group throughout the world. He may, in fact, forget some of the primary problems in building a taxonomic system. I feel that this may explain the deep differences in viewpoint of at least a few systematists.

Phylogenetic Approaches

It is my belief that systematics never can unravel the history of life in more than a general way, but that any formal system used by systematists should as closely approximate phylogeny as the limits of materials and human effort permit. As I pointed out over thirty years ago (Myers, 1930), any approximation to a "complete" systematic approach must be based on a study of every life process of the organisms concerned, in addition to anatomy and paleontology. For a long time it has been clearly evident that evolutionary rates differ profoundly, even in "closely related" species and genera (Myers, 1936, 1960), and that therefore "similarity is not synonymous with blood relationship" (Hennig, 1950; Kiriakoff, 1959), or at least not necessarily so. That such considerations make the evaluation of "relationship" based solely on the degree of morphological difference of existing forms a difficult and uncertain process should be universally recognized, but that this uncertainty should negate the phylogenetic importance of purely morphological or "typological" findings in recent organisms would be absurd.

It is also my belief that fine-spun categorical systems of dealing *either* with the phylogenetic classification of organisms *or* with the philosophical classification of phylogenetic methods are apt to be both misleading and transitory, simply because of the complexity of living matter and the way it behaves and must be studied. Life processes, at least in the present state of our knowledge, often do not lend themselves readily to definition or categorization. Erwin Schroedinger (1944) has pointed out that physical phenomena are not exact on the lowest level, and appear to be so merely because they are observed by man in a statistical way. Basic life processes compound not only the inexactness of physics, but also that of the living substances themselves. Evolution and systematics deal not only with whole organisms (again a compound of inexactness on a higher level) but also with populations of them, on what we might call a fourth level of inexactness. It is, then, no wonder that the processes studied by the systematist and evolutionist are often peculiarly difficult to bring into any exact system of knowledge.

Ideal Phylogenetic Taxonomy

An ideal phylogenetic systematics—which must be a recognizable if unattainable goal—would be nothing less than a history of life, using the word "history" in its broadest sense. It would be *complete* knowledge of all biological systems (including the physical ones upon which life is based) and all their changes throughout time— down through populations to each individual organism, and within the organism. Even if we were to restrict an ideal systematics to populations and their history, a *complete* knowledge would probably fill all gaps that we commonly think of as systematically important, and leave us nothing but imprecisely definable trends (or lines) upon which to base a classification. From this point of view, the ideal goal of systematic biological classification is a kind of definitionless chaos!

What is Typology?

We have not seen and will never see (or experiment upon) more than an infinitesimal portion of the organisms that we brashly propose to classify. Every biological study known to me, experimental or observational, has been based on the technique of *sampling* a comparatively few individuals and of *extrapolation* based on findings in the observed samples. In other words, our biological results are derived from and grouped about known samples. It is difficult, then, to see much philosophical difference, except in degree, between the "type" of the typologist and the "sample" of all biologists.

Basically then, I can see no easily definable difference between what Kiriakoff and Hennig call typological and phylogenetic taxonomists, except that the latter have perhaps thought somewhat more deeply about their field and indulge themselves in a complex, esoteric nomenclature intended to express that thinking. They are still essentially typologists, grouping their data about samples (experimental or observational) which may or may not be sufficient to indicate the true course of evolution, and which are philosophically the equivalent of the "types" of those they label as typologists. In other words, if we push the definition of "phylogenetic taxonomy" to its obvious conclusion—and ideal—it becomes something quite unattainable, and, in any sense which could be called absolute, all systematists and all biologists are typologists, and cannot help it.

Practical Problems

What, then, of a "phylogenetic taxonomy?" In the first place, we must realize that for a very long time, if not forever, the systematics of most groups of organisms must be done entirely on the basis of the living forms, and in the absence of direct experimental evidence. Experiment seems to be closed except on the subspecific (or specific) level, and the ecology and the very numbers of species make experiment on most of them impracticable. The imperfection of the geological record is still a very real barrier to extensive paleontological knowledge of all groups. Indeed, any really extensive knowledge of the fossil history of any group (even mammals) is far away and probably impossible. In bony fishes, for example, the origin of not a single one of the 30 or 40 orders of teleosts is discernible from the fossil record, nor do I have great hope that paleontology will ever demonstrate much in this regard. The same is true of most families of teleostean fishes. The numerous fossils known tell us little about the history of most existing taxa.

It is my belief that many taxonomists who never heard of the Hennig system are quite aware that similarity is not necessarily synonymous with "blood relationship," that paleontological evidence (if present and important) should be one of the main sources of any phylogenetic scheme, and that as many systematic characters as possible, drawn not only from

morphology, should be utilized. I have even pointed out the possibility of phylogenetically treating behavioral patterns (Myers, 1937), and Noble (1926, 1927) long ago utilized life-history and behavioral characters in amphibian taxonomy. I have included a discussion of time *versus* extent of divergence in lectures to my students for twenty years, yet I feel sure that the terminologically minded followers of Hennig would label most of my taxonomic papers as outside the pale of the elect group which they call "phylogenetic taxonomists!" Why? Simply because, in most of my work, like that of most systematists, all there is to depend on is the morphological similarity or difference in the dead specimen samples available to me—and I have not elected to use a terminology which seems largely superfluous and possibly not justified. I doubt exceedingly that there is today a really definable difference between phylogenetic and any other kind of taxonomy, short of pigeonholing by a non-evolutionist.

I do refuse to accept one of Hennig's tenets—that the "absolute value" (whatever that may mean in the philosophical sense) of taxa should be "based on their geological age." Any attempt to introduce either a pure time factor or evolutionary rates into formal taxonomy would be quite as disastrous as to insist that no phylogenetic taxonomy is possible without a paleontological record. On the one hand, evolutionary rates are unknown and incapable of investigation in most groups of organisms, while on the other, there is usually no usable fossil record. Sensible systematics can be based, in most instances, only on what we understand to be but an approximation to the truth, and the same is true of both classification and nomenclature.

Parenthetically, it should be said that it is for much the same kind of reason that I have opposed (Myers, 1950) the use of the interbreeding potential, as used by Mayr (1942), in recognition of species. We know nothing of it, and never will, with most living species. Interbreeding potential is an important biological principle, but I fail to see how the introduction of a guess about it in the usual systematic problem will in some magical manner make the systematics more "modern" and "dynamic." Moreover, evidence is accumulating that the interbreeding situation in birds, upon which Mayr's ideas were based, is not necessarily typical of other groups of animals. In fishes, interordinal hybrid larvae can be produced, and apparently some morphologically and behaviorally distinctive species happen to be easily hybridized in the laboratory (and produce fertile hybrids) but nevertheless maintain complete genetic isolation in the field, even when existing in the same habitat. Ichthyologists would certainly have *guessed* that such species *do not* hybridize, and that they could not hybridize. I do not see that their interbreeding potential (in the laboratory) should affect their recognition as species, for they behave naturally as genetically isolated systems.

Necessity for Inclusiveness

In other words, systematics, and classifications based on systematics, must be reasonably workable for *all* organisms, and not just for those few about which certain special types of information are available. It is the place of the systematist to find out all he can about the history of these organisms, but he cannot expect to express all he finds in any classification or formal systematization of knowledge. Any classification or system he uses should approximate what is known of relationships, but not to the extent of making the system or classification too complex or esoteric for general biological use. The species must remain as a taxon basic to all the rest, for it is a living, breathing entity (however we may or may not de-

fine it) which has a variable but reasonable number of biological characteristics in common with other such populations, no matter whether it is 10,000 or 2,000,000 years old, or whether we know anything of its characteristics, its paleontology, or its lineage. The general system now in use is based primarily on morphological resemblance, and has the advantage that most organisms can be placed in it with some assurance purely on the basis of anatomy, even the anatomy of an individual. If the basis were otherwise, a good part of the usefulness of classification would be lost, and, as a few biologists occasionally forget, classifications of any kind exist largely for human utilitarian purposes. Biological classification is an index, albeit one which attempts to make some features of presumed evolutionary relationship evident from the index itself.

Phylogenetic Taxonomy

The modern systematist still has to base the larger part of his work on morphology, but he must be alive to, and, if possible, use *all other avenues* of approach to his main problem, the history of life. Such a viewpoint, whether or not it agrees with the formalized tenets of Hennig or of anyone else, is, in my opinion, representative of modern phylogenetic taxonomy. It is not opposed to the Hennig school, or the typological school, or any other school. It embodies and makes use of all of them.

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An Evaluation of the Biotic Province Concept

Biotic provinces constitute one nominal and seemingly several conceptual approaches to the detection, organization, and characterization of biogeographic differentiation.

The chief difficulty encountered in consideration of this concept is distinguishing how the provinces *should* be regarded from what they can be and in turn from what they *are* regarded, compounded by the human variable that makes what *should* be, what *can* be and what *is* different in accordance with the individual performing the evaluation. Other students concerned with biotic provinces may well heartily disagree with views expressed here.

Biotic provinces are most frequently taken as areas of unique biotic attributes —areas with *taxonomically* distinctive floristic *and* faunistic features (e.g., Goldman and Moore, 1946; Smith, 1949; Blair

and Hubbell, 1948). They are distinguished primarily (or first) upon the basis of faunistic features because always floristic distinctions are amply borne out by faunistic distinctions, whereas the latter often occur without at least striking floristic parallel. Some authors (e.g., W. F. Blair, 1950; Dice, 1943) have based their biotic provinces on the sum of all environmental features, including both fauna and flora; even these are taxonomically and zoologically oriented.

So employed, biotic provinces differ from ecogeographic divisions in the taxonomic emphasis, and in the emphasis upon animals as a more delicate and plastic indicator than plants. Ecogeographic divisions, as for example, the Desert Scrub biociation of the southwestern United States, Baja California, and the central part of the Mexican plateau (e.g., Kendeigh, 1954: 167), emphasize gross habitat similarity keyed to climax or existent vegetation, and place little emphasis upon the enormous faunistic differences that may occur in different areas of the biociation. Biomes, and their biociation subdivisions, require floristic distinctiveness, whereas biotic provinces do not; only faunistic differences are *required* for the latter, although usually these faunistic differences are associated with floristic features. Perhaps the ranking of biome subdivisions (e.g., faciations) may closely approach the biotic province concept, but it is nevertheless a subdivision within what is at the outset a phytogeographic entity, whereas biotic provinces are, ideally, subdivisions of zoogeographic entities. Faciations of a single biociation are presumably more closely related to each other than any one is to any faciation of another biociation, but in reality their faunal relationship may very well not parallel the ecological relationship.

Biotic provinces seem to be the tool primarily of the systematist in zoology. They help him to guess range limits when few data are available and to guess whether differentiation is to be expected in two or more similar population samples from disjunct areas. They reflect paleozoogeography in a way ecogeographic divisions may not; to cite a theoretical example, two long distinct islands with virtually identical tropical vegetation features may after union into one island long retain sufficient faunistic individuality in the two formerly disjunct areas to warrant application of the biotic province label to each of the two zones.

So much for the theoretical role of biotic provinces. In actual practice they fall short of expectation, perhaps primarily because in fact no two species have the same optima for all environmental factors and, on top of this, the same geological history. Therefore no two species have identical ranges, whereas extensive agreement of range limits of numerous species is a necessary assumption in acceptance of the validity of the biotic province concept.

For ecologists and other non-taxonomists the biome and association concepts are fully adequate for all their needs. These concepts do not, however, fulfill the needs of systematists, for all these schemes of classification—even biociations and faciations (subdivisions of biomes), which parallel biotic provinces most closely—are subdivisions of ecological units, not of faunistic units. The part of the "desert scrub" biociation in central Mexico, for example, would certainly fall in a completely different faunistic region than that in Baja California. These two areas would be regarded as different faciations, but their faunistic relations would be far different from their floristic relations.

The best test of the validity of the biotic province for systematists or anyone else would come with accurate plotting of range of all species occurring in a given area. In practice, of course, this is as yet impossible even for the best-known groups of animals in the best-known areas. Therefore it behooves even the practicing systematist, as well as ecologists, to know

ecogeography and ecogeographic regions for his essential "guesstimate" purposes, for certainly, in the absence of definite knowledge, his greatest security in making estimates must lie in assuming correlation of distribution of any given animal species with *some* (even if guessed) floristic boundary. Fortunately the ranges of at least dominant plant species are relatively readily determined as compared with the ranges of animal species.

If the systematist *did* have full knowledge of the range of all or most or many animal species, as well as at least dominant plant species, would biotic provinces still be a useful tool? I doubt it. There would be a few areas recognizable as outstandingly distinctive that result from a relatively strong ecological and/or geographic isolation in the past and sometimes also in the present, but these "islands" would be surrounded by "seas" of individually different range boundaries coinciding at different points with equally different limits in any one of the many factors making up the environment. Biotic provinces, as commonly envisioned, do not, I think, exist. Peters (1955) approximated this conclusion in his analysis of the herpetofauna of western Mexico. In a vague way areas of different levels of faunistic distinction—strong, moderate, weak—could be recognized if all the facts were known, but it seems impossible to devise any one scheme of organization that would supply at a glance all the information of faunistic distinction *and* relationship a systematist needs and that sometimes has been expected from the concept of biotic provinces.

One of the hoped-for but in reality unattainable benefits of the biotic province concept can be gained far more securely by establishment through common consent or practice of a scale for measurement of faunistic relationship or distinction of two or more localities or areas on the basis of proportion of shared and excluded forms. This approach has long been used, of course, in support of the major Realms, Subrealms, Regions, and Subregions of classical zoogeography. It breaks down rapidly within any single continent as a system for establishment of boundaries of lesser zoogeographic areas, for the reason previously proposed that usefully distinct boundaries do not exist for them. Nevertheless the system can be extremely useful in contrasting any given sets of localities or areas, however small or large, near or distant. The time seems scarcely ripe now for setting up a universally applicable numerical scale for measurement of faunistic relation or distinction, and the levels appropriate for different zoogeographic hierarchies, but that such a system might well be devised, as a product of scales found applicable to small groups of organisms, seems not only possible but probable.

For example, the "faunistic relation factor" (FRF) for the lizard genus *Sceloporus* would be 1 in comparison of New York and Illinois, or Cairo of southern Illinois and Reading of southeastern Pennsylvania, because the composition of the *Sceloporus* fauna is identical in the two places. The FRF for *Sceloporus* at the *species* level would be 1 for Biloxi, Mississippi, and Cairo, Illinois, but 0 for the same places and genus at the *subspecific* level, since although the same single species of *Sceloporus* occurs at both localities the subspecies are different. For the same genus at the specific level, the FRF for Dallas, Texas, and Cairo, Illinois, is 0.5, since *undulatus* occurs at both places, and in addition *olivaceus* occurs at Dallas. For the same genus at the species level, the FRF for Panama and the United States is 0, since no species are shared. An FRF based upon several genera, or a whole family or group of families, orders, classes or phyla, at the subspecific, specific, generic or other higher ranking, would be of increasingly significant value in application to any one problem. It would at best never be conclusive, but it would be far more reliable as an indicator than any re-

finement of the current biotic province concept can seemingly ever be.

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A Brief Commentary on Simpson's Anatomy and Morphology: Classification and Evolution 1859 and 1959

G. G. Simpson (1959) has made another scholarly and significant addition to the literature of classification and evolution in his report for the Commemoration of the Centennial of the publication of the Origin of Species. As in the case of "The principles of classification and a classification of mammals" (1945), the complex interrelationships of evolution, phylogeny, and systematics are dealt with in a masterly way; but this time, in addition, Darwin's great influence upon the development of these subjects is critically analyzed. With the greater part of Simpson's report, I have nothing but praise; but there are a few matters which may be of great importance to the principles and methods of systematics which seem to be in need of further consideration.

Simpson finds Owen's (1843, 1848) suggestions in regard to the criteria to be used in the recognition of special homologies "extremely ambiguous." He points out, further, that special homology, as of 1843, was devoid of explanatory content and therefore unsatisfying. To be sure it was Darwin (1859) whose work brought about the general acceptance of an evolutionary explanation for these homologies as probably being due to common ancestry.

In his further discussion Simpson states that when Darwin explained homologues as due to common ancestry, "he implicitly provided a theoretically objective criterion as to what is and what is not a homologue. The common ancestry that not only explains, but in this view also defines homologues did objectively exist if evolution is true." Simpson goes on to say that some later authors have insisted that Owen's criteria are more objective and Darwin's "merely subjective." "This is curious because many of the data of *both*, the anatomical resemblances, are identical, and the additional data (mainly paleontological) pertinent to Darwin's definition are equally observational. The criteria for interpretation of those data were completely subjective for Owen; what constitutes 'essential structural similarity' can only be subjective or intuitive. It is not even an opinion *about* a definable reality, which judgment of common ancestry is, at worst."

Though discussion of the relative "objectivity" of Owen's and Darwin's criteria of homology may be painful to some, I wish to try to resolve some of the misunderstandings which have developed in regard to morphology's "central conception." In the first place neither I (1947) nor Blackwelder and I (1952) have ever stated or implied that Darwin's criteria of homology were "merely subjective." We have said repeatedly, that a judgment in

regard to the homology of certain parts can only be made after an appraisal of the amounts and kinds of similarities which exist among those parts, together with such additional information as is available in regard to the space and time distribution of organisms possessing such parts. We agree with Simpson that the *data* required to justify a conclusion of homology may be the same, but we disagree that Darwin's criteria are more objective in any proper sense of the word, *even though the common ancestry did exist!* For the probability of drawing a correct conclusion in regard to common ancestry is based not on direct knowledge of such ancestry, but on an evaluation of the kinds of similarities which exist between the structures compared. The view which we have upheld implies that it is indeed more "objective" to classify existing organisms on the basis of their natures with due regard to the available knowledge of their hereditary constitutions, and to classify fossil organisms on the basis of their fossil characters. The principles and procedures are very much the same whether existing organisms without known fossils, or extinct organisms without modern descendants, are to be classified; or whether, finally, recent and former organisms with essential similarities of structure are to be grouped together. These structural characters can be described with whatever degree of completion the available materials permit; this is the first and can be the most objective basis for taxonomy; following upon this the selection and weighting of the characters may lead to one or more of several possible phylogenetic or "genealogical" arrangements of the organisms concerned. In my view, this second step in classification is less certain and less objective than the first, for the very reason that it does require an explanation which may or may not be true. However desirable and satisfying these explanations are, their validity is predicated on further knowledge which is often minimal or unobtainable and therefore they should, by right, be considered more subjective than the straightforward description and comparison of the characters available for study. The whole of Darwin's chapter on the "Mutual affinities of organized beings," supports this conclusion; and, I believe, justifies the terms "essential similarities" or "essential natures" as we and others have used them. Darwin said, "We are forced to trace community of descent by resemblances of any kind." This to us is a more honest and revealing statement than those which, by omission, seem to imply that homology can be recognized by ancestry directly. And if, as all must agree, we are "forced" to use these resemblances, they certainly become "essential" for the purpose. But not all resemblances in structure are equally reflective of common ancestry and much of that chapter in Darwin's Origin is given to a discussion of the selection of criteria which may be the more useful in phylogenetic study. Here again we are justified in using the term "essential similarities," for those which are apparently the more conservative are the essential ones required in the attempts to determine remote community of descent.

Speaking of Darwin's chapter which provided the chief subjects for Simpson's commentary, we wish to call attention to a possible misunderstanding which may arise from his treatment of "propinquity of descent." It seems fair to conclude from Simpson's discussion that he believed Darwin was supporting the principle of classifying on the basis of "propinquity of descent." This was not true even at the time of the first edition of the Origin.

Darwin used several phrases in his explanation of how the natural system of classification may be founded on "descent with modification." One of these phrases is "propinquity of descent." In the first edition of the Origin of Species and the chapter on "Mutual affinities of organic beings," the phrase "propinquity of descent" is used once and the phrase "com-

munity of descent" three times. In the sixth edition "propinquity of descent" has been omitted and is replaced by "community of descent." Yet Simpson quotes only Darwin's "propinquity of descent." The actual frequency of usage is not the decisive thing here; it is rather the meaning which should be attached to these terms and particularly the meaning that Darwin attached to them. We assume that the term "community of descent" implies only common ancestry, without specification in regard to its recency. On the other hand, the term "propinquity of descent" implies, or should imply, nearness of common ancestry, or relative recency of common origin. If Simpson means to imply that Darwin's "new taxonomic principle" was really to classify on recency of common origin, he is wrong, except in the classification of varieties. Darwin stated that, "In classing varieties, I apprehend that if we had a real pedigree, a genealogical classification would be universally preferred. . . ." This would be a classification based on propinquity of descent, but in all other cases Darwin makes it very clear that he was not recommending such a classification. "I believe that the *arrangement* of the groups within each class, in due subordination and relation to each other, must be strictly genealogical in order to be natural; but that the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders."

There are several similar passages in this chapter of the Origin, all of which carry the same meaning and make it clear that "the amount of modification which the different groups have undergone has to be expressed by ranking them under different so-called genera, subfamilies, families, sections, orders, and classes." Thus Darwin definitely did not classify on "propinquity of descent" as Simpson would have us believe, nor did he recommend any such principle for classification, except for varieties as noted above.

Additional statements regarding the importance of recency of common origin in systematics may be found in the reports of Bader (1958), Bigelow (1956, 1958), and Ehrlich (1958).

In summary, we question Simpson's claims regarding the objectivity of the ancestral criterion of homology and show that Darwin neither accepted nor endorsed the principle of classifying on the basis of propinquity of descent.

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